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THE PHYSIOLOGY OF MAN;

DESIGNED TO REPRESENT

THE EXISTING STATE OF PHYSIOLOGICAL SCIENCE,

AS APPLIED

TO THE FUNCTIONS OF THE HUMAN BODY.

BY

AUSTIN FLINT, Jr., M.D.,

PROFESSOR OF PHYSIOLOGY AND PHYSIOLOGICAL ANATOMY IN THE BELLEVUE HOSPITAL MEDICAL COLLEGE, NEW YORK; ATTENDING PHYSICIAN TO THE BELLEVUE HOSPITAL; CONSULTING PHYSICIAN FOR THE CLASS OF NERVOUS DISEASES TO THE BUREAU OF MEDICAL AND SURGICAL RELIEF FOR OUT-DOOR POOR, BELLEVUE HOSPITAL; FELLOW OF THE NEW YORK ACADEMY OF MEDICINE; MEMBER OF THE MEDICAL SOCIETY OF THE COUNTY OF NEW YORK, ETC., ETC.

vol 4

NERVOUS SYSTEM.

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1873.

PREFACE.

There is, probably, no subject connected with human physiology, which has engaged the attention of experimentalists and philosophic writers so much as the nervous system, especially within the last few years. The author has, from the first, looked upon this division of the work as the most important and the most difficult of all, and feels that this volume will be regarded with more critical interest than any one of the series; and if he has succeeded, even in a measure, in giving, in it, a satisfactory representation of our present positive knowledge, no apology is necessary for the length of time occupied in its preparation. For two and a half years, he has been almost unremittingly engaged in writing this volume, and has endeavored to overcome, rather than avoid, the difficulties which have presented themselves in the investigation of important questions, which are as yet regarded by many as unsettled.

A great part of the inevitable delay which has attended the publication of this part of the work has been due to the difficulty in this country of consulting rare and important memoirs. When it is stated that every citation

has been made after a careful study of the original publication, any one acquainted with the literature of the nervous system will appreciate the amount of labor involved simply in bibliographical research; but in this department, more than in any other, it is necessary to avoid taking experiments and opinions at second-hand. The experience of many years, as an experimental physiologist and a practical teacher, has enabled the author to verify many of the important facts stated in this volume, and has led to some original observations, which appear in the body of the work.

The present volume treats of the physiological anatomy and the functions of the nervous system, as they appear to a practical physiologist, accustomed to accept nothing that is not capable of positive demonstration or well-sustained inference. Adhering conscientiously to the positive method of study, the author has endeavored to present an account of the nervous system, which, though it will undoubtedly be extended by future investigations, is made up mainly of statements of facts that will probably not undergo serious modification, as we advance in our knowledge of the subject. He has considered the properties and functions of the cerebro-spinal and sympathetic nervous systems, mainly from this point of view; and has touched but slightly upon psychology, which has long been considered a science by itself. The special senses have been deferred, to be taken up in the fifth and last volume of the series.

The physiological anatomy of the nervous system is regarded by the author as an indispensable preparation for the study of its functions. The most reliable recent

works upon histology contain, of course, much that is of no great physiological interest or importance, and the best anatomical treatises do not generally give a description of parts with particular reference to their physiology. To facilitate the thorough comprehension of the subject, the author has carefully detailed certain anatomical points, a familiarity with which is necessarily involved in an accurate study of nervous physiology.

The publishers of this series, having lately issued Prof. Hammond's treatise on Nervous Diseases, are desirous of presenting a complete work on the "Physiology and Pathology of the Nervous System." Both Prof. Hammond and the author of this volume heartily concur in this plan. Though the full consideration of the physiology of the nervous system would perhaps be out of place in a treatise on nervous diseases, a thorough knowledge of its functions is none the less important as a preparation for the intelligent study of its pathology. The present volume was written as one of the series on the "Physiology of Man," but will also be issued as the first volume of a complete work on the Physiology and Diseases of the Nervous System. It is proper to state that the two volumes thus published were written independently of each other, and that Prof. Hammond is in nowise responsible for the author's views upon physiology, nor for any errors or defects that may be found in his part of the work. The reader, however, will find few points upon which there is any radical or important difference of opinion; but where these differences occur, they have been frankly stated, and each author is solely responsible for his own opinions and statements.

Finally, the author presents this volume, with the simple statement that he has made an honest attempt to compass the great subject to which it is devoted, the magnitude and importance of which he never appreciated so fully as at the present moment. In the preparation of this volume, it was expected to include in it the special senses, and chapters upon touch, smell, and sight, were written, so that at least one-fifth of the last volume of the original series is already completed. The fifth volume is therefore so far advanced, that it is hoped that the entire work will be finished within a year. The last part will be devoted to the Special Senses and Generation.

New York, May, 1872.

CONTENTS.

CHAPTER I.

PHYSIOLOGICAL DIVISIONS AND STRUCTURE OF THE NERVOUS SYSTEM.

CHAPTER II.

MOTOR AND SENSORY NERVES.

CHAPTER III.

GENERAL PROPERTIES OF THE NERVES.

CHAPTER IV.

SPINAL NERVES—MOTOR NERVES OF THE EYEBALL.

CHAPTER V.

MOTOR NERVES OF THE FACE.

CHAPTER VI.

SPINAL ACCESSORY AND SUBLINGUAL NERVES.

CHAPTER VII.

TRIFACIAL, OR TRIGEMINAL NERVE.

CHAPTER VIII.

PNEUMOGASTRIC, OR PAR VAGUM NERVE.

CHAPTER IX.

PHYSIOLOGICAL ANATOMY AND GENERAL PROPERTIES OF THE SPINAL CORD.

CHAPTER X.

ACTION OF THE SPINAL CORD AS A CONDUCTOR.

CHAPTER XI.

ACTION OF THE SPINAL CORD AS A NERVE-CENTRE.

CHAPTER XII.

THE CEREBRAL HEMISPHERES.

CHAPTER XVI.

SLEEP.

PHYSIOLOGY OF MAN.

CHAPTER I.

PHYSIOLOGICAL DIVISIONS AND STRUCTURE OF THE NERVOUS SYSTEM.

General considerations—Divisions of the nervous system—Physiological anatomy of the nervous tissue—Anatomical divisions of the nervous tissue—Medullated nerve-fibres — Simple, or non-medullated nerve-fibres — Gelatinous nerve-fibres (fibres of Remak)—Accessory anatomical elements of the nerves—Branching and course of the nerves—Termination of the nerves in the muscular tissue—Termination of the nerves in glands—Terminations of the sensory nerves—Corpuscles of Pacini, or of Vater—Tactile corpuscles—Terminal bulbs—Structure of the nerve-centres—Nerve-cells—Connection of the cells with the fibres and with each other—Accessory anatomical elements of the nerve-centres—Composition of the nervous substance—Regeneration of the nervous tissue—Reunion of nerve-fibres.

The nervous system is anatomically distinct in all animals, except those lowest in the scale of being. It is useless to speculate upon the question of the existence of matter endowed with properties analogous to those observed in the nervous system of the higher animals, in beings so low in their organization as to present no divisions into anatomical elements; for the present condition of physiological science does not admit of the recognition of functions without organs. All animals that present any thing like nervous functions present also an anatomically distinct nervous system. Within certain limits, the perfection of the animal organization depends upon the general development of the nervous system.

High in the animal scale, as in the warm-blooded ani-

mals, the general development of this system presents little, if any, variation; but special attributes are coexistent with the development of special organs. The development in this way of particular portions of the nervous system is in accordance with the particular conditions of existence of different animals; it is a necessary part of their organization, and is not dependent upon education or intelligence. Examples of this are in the extraordinary development of the sense of sight, hearing, or smell, in different animals. There are animals in which these special senses possess a delicacy of perception to which man, even with the greatest amount of intelligent education, can never attain; but man, possessing a nervous organization not superior to that of other warm-blooded animals in its general development, and inferior to many in the development of special organs, stands immeasurably above all other beings, by virtue of the immense preponderance of what is known as the encephalic portion of the nervous system.

These brief general considerations will convey some idea of the physiological importance of the nervous system; of the care which should be exercised in its study; and of the great interest attached to it, from the fact that the most complex and important of its functions belong to human physiology, and to human physiology alone.

We can best define what is to be included under the head of the nervous system, by citing certain of its prominent and well-established properties and functions.

1. The nervous system is anatomically and physiologically distinct from all other systems and organs in the body. It receives impressions made upon the terminal branches of its sensory portion, it conveys stimulus to parts, determining and regulating the operation of their functions; but its physiological properties are inherent, and it gives to no tissue or organ its special "irritability" or the power of performing its particular function.[1]

[1] We have already discussed the independence of what is called "nervous

2. The nervous system connects into a coördinated organism every part of the body. It is the medium through which all impressions are received. It animates or regulates all movements, voluntary and involuntary. It regulates the functions of secretion, nutrition, calorification, and all the processes of organic life.

In addition to its functions as a medium of conduction and communication, the nervous system, in certain of its parts, is capable of receiving impressions and of generating a stimulating influence, or force, peculiar to itself. As there can be no physiological connection or coördination of different parts of the organism, having an active function, without nerves, there can be no unconscious reception of impressions giving rise to involuntary movements, no appreciation of impressions, general, as in ordinary sensation, or special, as in sight, smell, taste, or hearing, no instinct, volition, thought, or even knowledge of existence, without nerve-centres.

Possessing, as it does, these varied properties and functions, it is evidently of the greatest physiological importance that the anatomical characters of the nervous system should be most carefully studied, with a view, if possible, of connecting certain of the nervous properties with peculiarities in structure. It is also important to subdivide the system, as regards general properties and functions, as well as with reference to the special office of particular parts. With this end in view, we will point out, first, the great anatomico-physiological divisions common to nervous matter wherever it exists, and afterward, the subdivisions of the system as regards special functions.

Divisions of the Nervous System.

Nervous matter, whatever may be its special function, presents two great divisions, each with distinct anatomical

irritability," in treating of the properties of the muscles. See vol. iii., Movements, p. 463.

as well as physiological differences.' One of these divisions presents the form of fibres, or tubes. This kind of nervous matter is incapable of generating a force or stimulus, and serves only as a conductor. The other division is in the form of cells, and this kind of nervous matter alone is capable of generating the so-called nervous force.

The nervous matter is divided into two great systems, as follows:

1. The cerebro-spinal system, composed of the brain and spinal cord with the nerves directly connected with these centres. This system is specially connected with the functions of relation, or of animal life. The centres preside over general sensation, the special senses, voluntary and some involuntary movements, intellection, and, in short, all of the functions that characterize the animal. The nerves serve as the conductors of impressions known as general or special sensations, and of the stimulus that gives rise to voluntary and certain involuntary movements, the latter being the automatic movements connected with animal life.

2. The sympathetic, or organic system. This system is specially connected with the functions relating to nutrition, operations which have their analogue in the vegetable kingdom, and are sometimes called the functions of vegetative life. Although this system presides over functions entirely distinct from those characteristic of and peculiar to animals, the centres of this system all have an anatomical and physiological connection with the cerebro-spinal nerves.

The cerebro-spinal system is subdivided into centres presiding over movements and ordinary sensation, and centres capable of receiving impressions connected with the special senses, such as sight, audition, olfaction, and gustation. The nerves which receive these special impressions and convey them to the appropriate centres are more or less insensible to ordinary impressions. The organs to which these special nerves are distributed are generally of a complex and peculiar structure, and present numerous accessory parts which

are important and essential in the transmission of the special impressions to the terminal branches of the nerves.

In treating of the nervous system, we will consider first the physiological anatomy of the nervous tissue; next, the general properties of the cerebro-spinal system; next, the functions of different portions of this system connected with motion, ordinary sensibility, intellection, etc.; next, the functions of the sympathetic, or organic system of nerves; and finally, the special senses, with the physiological anatomy and mechanism of the accessory parts.[1]

Physiological Anatomy of the Nervous Tissue.

The physiological anatomy of the nervous system natually divides itself into two sections; one embracing what is called the general anatomy of the nervous tissue, and the other, the arrangement of this tissue in special organs, as far as this is connected with their functions.

The intimate structure of the different portions of the nervous system may now be regarded as tolerably well understood, at least as far as those anatomical points bearing on physiology are concerned. The connection between the nerve-cells and the fibres and the modes of termination of the motor filaments in the muscles are points nearly, if not quite, settled; and the terminations of sensory filaments in integument and mucous membranes have lately been investigated very thoroughly, and with quite positive and satisfactory results. These anatomical points are especially connected with the general properties of the nervous system, both as a generator of the so-called nerve-force and as a conductor.

The arrangement of the nervous elements in special organs, as in the brain and spinal cord, has not been so successfully investigated, and presents immense difficulties in its study; and we can hardly hope to acquire any thing like

[1] The special senses will be fully considered in the fifth and last volume of this series.

a definite and thorough knowledge of the functions of these parts, until we have much more positive information concerning their anatomical characters.

Anatomical Divisions of the Nervous Tissue.—The physiological division of the nervous system into nerves and nerve-centres is pretty well carried out as regards the anatomical structure of these parts. The two great divisions of the system, anatomically considered, are into nerve-cells and nerve-fibres.

The nerve-cells, as far as we know, are the only parts capable, under any circumstances, of generating the nerve-force ; and, as a rule, they cannot receive impressions in any other way than through the nerve-fibres. There are, however, some exceptions, either apparent or real, to this rule, as in the case of direct irritation of the ganglion of the tuber annulare, and the sympathetic ganglia, which seem sensible to direct irritation ; but the cells of most of the ganglia belonging to the great cerebro-spinal axis are insensible to direct stimulation and will only receive impressions conducted to them by the nerves.

The nerve-fibres act only as conductors, and are incapable of generating nerve-force. There is no exception to this rule, but there are differences in the properties of certain fibres. The nerves generally, for example, will receive direct impressions, the motor filaments conducting these to the muscles and the sensory filaments conveying the impressions to the centres. These fibres will also conduct the force generated by the nerve-centres. But there are many fibres, such as those composing the white matter of the encephalon and the spinal cord, that are insensible to direct irritation, while they will convey to the centres impressions made by the sensitive nerves, and will conduct to the motor nerves stimulus generated by nerve-cells.

Structure of the Nerves.—There are few anatomical ele-

ments that present greater variations in size and appearance than the nerve-fibres. Certain fibres found in the course of the nerves between the muscles are as large as $\frac{1}{1250}$ of an inch, have dark borders, and possess three well-marked structures; viz., a tubular membrane, medullary contents, and an axial band; others, with the same structure, are only $\frac{1}{25000}$ of an inch in diameter; others have only the medullary covering and the axial band; and others present the axial band alone. Most of these anatomical elements have essentially the same physiological conducting properties; the variations in their structure depending upon differences in their anatomical relations. In view of these facts, it will be convenient to adopt some anatomical classification of the fibres.

In the most simple classification of the nerve-fibres, they are divided into two groups; one embracing those fibres which have the conducting element alone, and the other presenting this element surrounded by certain accessory structures. In the course of the nerves, the simple fibres are the exception, and the other variety is the rule; but as the nerves are followed to their terminations in muscles or sensitive parts, or are traced to their origin in the nerve-centres, we find that they lose one or another of their adventitious elements. These two varieties we shall term: 1. The medullated fibres, and 2. The simple, or non-medullated fibres.

Medullated Nerve-fibres.—These fibres are so called by French and German writers because, in addition to the axis-cylinder, or conducting element, they contain, enclosed in a tubular sheath, a soft substance called the medulla. This substance is strongly refractive and gives the nerves a peculiar appearance under the microscope, from which they are sometimes called the dark-bordered nerve-fibres. As the whole substance of the fibre is enclosed in a tubular membrane, these are frequently spoken of as nerve-tubes.

If the nerves be examined while perfectly fresh and un-

changed, their anatomical elements appear in the form of simple fibres with strongly accentuated borders. The diameter of these fibres is from $\frac{1}{2500}$ to $\frac{1}{1700}$ of an inch.[1] To observe the fibres in this way, it is necessary to take a nerve from an animal just killed and examine it without delay. In a very short time the borders become darker and the fibre assumes an entirely different appearance. By the use of certain reagents, it can be demonstrated that a medullated nerve-fibre is composed of three distinct portions; viz., a homogeneous sheath, a semi-fluid matter contained in the sheath, and a delicate central band.

The tubular sheath of the nerve-fibres is a somewhat elastic, homogeneous membrane, never striated or fibrillated, and presenting generally oval nuclei, with their long diameter in the direction of the tube. This is sometimes called the neurilemma, a name, however, which is more generally applied to another membrane. It is sometimes spoken of, also, as the "limiting membrane of Valentin," or "the sheath of Schwann." In its chemical and general properties, this membrane resembles the sarcolemma, though it is less elastic and resisting. It exists in all the medullated nerve-fibres, large and small, except those in the white portions of the encephalon and spinal cord. It is not certain that it does not exist in the small, non-medullated fibres, though its presence here has never been satisfactorily demonstrated.[2] As we before remarked, the tubular membrane cannot be seen in the perfectly fresh nerves; and even after they have become changed by desiccation, its demonstration requires the use of reagents. In the ordinary medullated fibres, however, it may be isolated by boiling the nerve in absolute alcohol and then in acetic acid, or by treating it with cold caustic soda. By then boiling the nerve for an instant in the caustic soda, fragments of the tube may be isolated, when they resemble the membrane forming the canals of the kidney. Another

[1] LITTRÉ ET ROBIN, *Dictionnaire de médecine*, Paris, 1865, Article, *Nerveux.*

[2] KÖLLIKER, *Éléments d'histologie humaine*, Paris, 1868, p. 315.

method is to treat the nerve with fuming nitric acid, afterward adding a solution of caustic potash. The fatty substance is thus discharged in small drops, the central band is dissolved, and the empty sheath is seen, swollen and tinged with yellow. These are the processes employed by Kölliker, who demonstrates in this way the presence of nuclei.[1]

The medullary substance fills the tube and surrounds the central band. This is called by various names; as myeline, white substance of Schwann, medullary sheath, nervous medulla, etc. It does not exist either at the origin of the nerves in the gray substance of the nerve-centres or at the peripheral termination of the nerves, and is probably not an essential conducting element. When the nerves are perfectly fresh, this substance is transparent, homogeneous, and strongly refracting, like oil; but as the nerves become altered by desiccation, the action of water, acetic acid, and various other reagents, it coagulates into an opaque, granular mass. The consistence of this substance gives to the medullated fibres a very peculiar appearance. The tubular membrane being very thin and not elastic, the white substance, by very slight pressure, is made to fill the tubes irregularly, giving them a varicose appearance, which is entirely characteristic. In examining a preparation of the nervous tissue, large drops, coagulated in irregular shapes, are seen scattered over the field, and frequently fringing the divided ends of the tubes. In the white substance of the encephalon and spinal cord, where the tubular membrane is wanting, the varicose appearance of the fibres is more remarkable than in any other situation.

The axis-cylinder is, in all probability, the essential anatomical element of the nerves. It exists in all the nerves except in those termed gelatinous fibres, or fibres of Remak, which will be described hereafter. In the ordinary medullated fibres, the axis-cylinder cannot be seen in the natural condition of the tissue, because it refracts in the same man-

[1] Kölliker, *op. cit.*, p. 318.

ner as the medullary substance, and it cannot be demonstrated afterward, on account of the opacity of the coagulated matter. If a fresh nerve, however, be treated with strong acetic acid, the divided ends of the fibres will retract, leaving the axis-cylinder, which is but slightly affected by reagents. It then presents itself in the form of a pale, slightly-flattened band, with outlines tolerably regular, though slightly varicose at intervals, somewhat granular, and sometimes very finely striated in a longitudinal direction. This band is elastic, but not very resisting. Its granules are excessively pale. What serves to distinguish it from all other portions of the nerve-fibre is its insolubility in most of the reagents employed in anatomical investigation. It is slightly swollen by acetic acid, but is dissolved after prolonged boiling. If a solution of carmine be added to the nervous tissue, the axis-cylinder only is colored. It has been remarked that the nerve-fibres treated with nitrate of silver present in the axis-cylinder well-marked transverse striations. This was observed by Frommann,[1] and has since been confirmed by Grandry.[2] The latter observer is disposed to regard both the nerve-cells and the axes of the fibres as composed of two substances, the limits of which are marked by the regular striæ developed by the nitrate of silver. This, however, is a point of purely anatomical interest. The presence of regular and well-marked striæ in the axis-cylinder after the addition of a solution of nitrate of silver and the action of light cannot be doubted; but it has not yet been determined beyond question whether these markings be entirely artificial, or whether the axis-cylinder be really composed of two kinds of substance.

A still more important question with regard to the inti-

[1] FROMMANN, *Ueber die Färbung der Binde- und Nervensubstanz des Rückenmarkes durch Argentum nitricum und über die Struktur der Nervenzellen.—Archiv für pathologische Anatomie und Physiologie*, etc., Berlin, 1864, Bd. xxxi., S. 129, *et seq.—Zur Silberfärbung der Axencylinder*, ibid., S. 151, *et seq*

[2] GRANDRY, *De la structure intime du cylindre de l'axe et des cellules nerveuses.—Journal de l'anatomie*, Paris, 1869, tome vi., p. 289, *et seq.*

mate structure of the axis-cylinder refers to the longitudinal striations. These are observed in many fibres, but they are not constant. Some authors have adopted the view that the markings are produced by fibrillæ, analogous to the fibrillæ of the muscular fibres, in all the fibres, as well as in those of the retina, olfactory, and some of the sympathetic nerves.[1] In the organs of special sense, there can be no doubt of the existence of fibrillæ; but this is by no means so clearly demonstrable in the general system of nerves. Still, it is necessary to take into consideration, in this connection, certain facts with regard to the origin of the nerve-fibres in the cells and their ultimate distribution in sensitive parts. In the final distribution of sensitive nerves, we shall see that the fibres break up into filaments resembling fibrillæ, and although the fibrillated character of the poles of the nerve-cells is not unreservedly accepted by anatomists, many observers positively state that such is their structure. In the present condition of the science, we cannot do more than state that, while a fibrillated structure has perhaps been shown in the nerves of some of the lower orders of animals, its existence in man and the mammalia is somewhat doubtful.

The diameter of the axis-cylinder is about one-half or one-third that of the tube in which it is contained. The various appearances which the nerve-fibres present under different conditions are represented in Fig. 1.

Simple, or Non-medullated Nerve-Fibres.—These fibres are found very largely distributed in the nervous system. In the last edition of what is perhaps the most authoritative work on histology, it is stated that "the more we advance in our researches, the more evident it becomes that, in man and the higher classes of animals, nerve-fibres without the white substance are very widely distributed."[2] However,

[1] SCHULTZE, in STRICKER, *Manual of Human and Comparative Histology*, London, 1870, vol. i., p. 147, *et seq.*

[2] KÖLLIKER, *op. cit.*, p. 322.

when we come to study the structure and relations of these small fibres, which seem in many instances to be simple prolongations, without alteration, of the axis-cylinder of the medullated fibres, it will be seen that they are chiefly found in the peripheral terminations of the nerves and in the fila-

Fig. 1.

Nerve-fibres from the human subject, magnified 350 diameters; four small fibres, of which two are varicose, one medium-sized fibre with borders of single contour, and four large fibres; of the latter, two have a double contour, and two contain granular matter. (Kölliker, *Handbuch der Gewebelehre*, Leipzig, 1867, S. 239.)

ments of connection of the fibres with the cells. The study of the fibres in these relations constitutes the most important part, physiologically, of the anatomy of the nerves, and presents the greatest difficulties in the way of direct observation; and, for that reason, we shall treat of these questions separately, and defer until then the full consideration of the non-medullated fibres.

Gelatinous Nerve-Fibres (*Fibres of Remak*). — These fibres are entirely different in their anatomy from either of the varieties of fibres just considered. They are found chiefly in the sympathetic system, and in that particular portion of

this system connected with involuntary movements. For instance, these fibres are very abundant in the gray filaments sent to parts provided with non-striated muscular fibres and endowed with undoubted motor properties; but they are not found in the white filaments of the sympathetic, which seem to be incapable of exciting movements.[1]

There is considerable difference of opinion among physiologists with regard to the gelatinous filaments. Some are disposed to regard them as elements of connective tissue, not endowed with properties characteristic of nerves, while others consider that they are nerve-fibres, probably possessing functions distinct from those of the fibres of different structure. The first opinion was formerly held by Kölliker, who states, in one of the early editions of his work on Microscopic Anatomy, that all of the fibres of Remak are "only a form of connective tissue;"[2] but in a later edition, he admits that the nucleated fibres of the great sympathetic, which resemble embryonic nervous elements, are really nerve-fibres.[3] This is the view now adopted by the best anatomists. While it is certain that elements of connective tissue exist in the nerves, and have been mistaken for true nerve-fibres, there are in the nerves, particularly in those belonging to the great sympathetic system, fibres exactly resembling the nerve-fibres of the embryon. These are the true gelatinous nerve-fibres, or fibres of Remak. It is stated that the nerves generally have this structure up to the fifth month of intrauterine life, and that in the regeneration of nerves after division or injury, the new elements assume this form before they arrive at their full development.[4]

The true gelatinous nerve-fibres present the following characters: They are flattened, with regular and sharp borders, grayish and pale, presenting numerous very fine

[1] REMAK, *Observationes de Systematis Nerv. Struct.*, Berolini, 1838, p. 5.

[2] KÖLLIKER, *Microscopic Anatomy*, London, 1860, p. 254.

[3] KÖLLIKER, *Éléments d'histologie humaine*, Paris, 1868, p. 432.

[4] LITTRÉ ET ROBIN, *Dictionnaire de médecine*, Paris, 1865, Article, *Nerveux.*

granulations, and a number of oval, longitudinal nuclei, a characteristic which has given them the name of nucleated nerve-fibres. The diameter of the fibres is about $\frac{1}{8000}$ of an inch. The nuclei have nearly the same diameter as the fibres, and are about $\frac{1}{1200}$ of an inch in length;[1] they are finely granular, and present no nucleoli. The fibres are rendered pale by the action of acetic acid, but they are slightly swollen only, and present, in this regard, a marked contrast with the elements of a connective tissue. The microscopical appearances of these fibres, which are strongly characteristic, are represented in Fig. 2.

Fig. 2.

Fibres of Remak, magnified 300 diameters. With the gelatinous fibres, are seen two of the ordinary, dark-bordered nerve-fibres. (Littré et Robin, *Dictionnaire de médecine*, Paris, 1865, p. 999.)

Accessory Anatomical Elements of the Nerves.—The nerves present, in addition to the different varieties of true nerve-fibres just described, certain accessory anatomical elements common to nearly all of the tissues of the organism, such as connective tissue, blood-vessels, and perhaps lymphatics, though these have never been demonstrated, except in the nerve-centres.

Like the muscular tissue, the nerves are made up of their true anatomical elements, the nerve-fibres, held together into primitive, secondary, and tertiary bundles, and so on, in proportion to the size of the nerve. The primitive fasciculi are surrounded by a delicate membrane, described by Robin under the name of *périnèvre*,[2] but which had been already noted by other anatomists under different names.[3] This membrane is homoge-

[1] Littré et Robin, *loc. cit.*

[2] Littré et Robin, *Dictionnaire de médecine*, Paris, 1865, Article, *Périnèvre.*

[3] Kölliker, *Éléments d'histologie humaine*, Paris, 1868, p. 317.

neous or very finely granular, sometimes marked with longitudinal striæ, and possessing elongated nuclei, finely granular, from $\frac{1}{2000}$ to $\frac{1}{1000}$ of an inch in length by from $\frac{1}{8000}$ to $\frac{1}{5000}$ of an inch wide. The thickness of the membrane is from $\frac{1}{12000}$ to $\frac{1}{8000}$ of an inch. It commences at the point where the nerve-fibres emerge from the white portion of the nervous centres, and extends to their terminal extremities, being interrupted by the ganglia in the course of the nerves. This membrane generally envelops a primitive fasciculus of fibres, branching as the bundles divide and pass from one trunk to another; but it is sometimes found surrounding single fibres. An important anatomical fact connected with this membrane is that it is never penetrated by blood-vessels, the smallest capillaries of the nerves ramifying in its substance, but never passing through to the individual nerve-fibres. Within the perinerve, are sometimes found elements of connective tissue, but never any other of the accessory anatomical elements of the nerves.[1]

The amount of fibrous tissue in the different nerves is very variable and depends upon the external conditions to which they are subjected. In the nerves within the bony cavities, where they are entirely protected, the fibrous tissue is very scanty; but in the nerves between muscles, we find a tolerably strong investing membrane, or sheath surrounding the whole nerve and sending processes into its interior, which envelop smaller bundles of fibres. This sheath is formed of inelastic fibres with small elastic fibres and nucleated connective-tissue fibres. These latter may be distinguished from the gelatinous nerve-fibres by the action of acetic acid, which swells and finally dissolves them, while the nerve-fibres are but slightly affected.

The late researches of Sappey have shown that the structure of the fibrous sheath of the nerves possesses certain important anatomical peculiarities. The greatest part of this membrane is composed of bundles of white, inelastic

[1] Littré et Robin, *loc. cit.*

tissue, interlacing in every direction; but it contains also numerous elastic fibres, adipose tissue, a net-work of arteries and veins, and "*nervi-nervorum*," which are to these structures what the vasa-vasorum are to the vessels. The adipose tissue is constant, being found even in extremely emaciated persons.[1]

The vascular supply to most of the nerves is rather scanty. The arteries break up into a plexus of very fine capillaries, arranged in oblong, longitudinal meshes surrounding the fasciculi of fibres; but they never penetrate the perinerve and come in contact with the ultimate nervous elements. The veins are rather more voluminous, and follow the arrangement of the arteries. It is not certain that the nerves in their course contain lymphatics; at least these vessels have never been demonstrated in their substance.

Branching and Course of the Nerves.—The ultimate nerve-fibres in the course of the nerves have no connection with each other by branching or inosculation. A bundle of fibres frequently sends branches to other nerves and receives branches in the same way; but this is simply the passage of fibres from one sheath to another; the ultimate fibres themselves maintaining throughout their course their integrity and individual physiological properties. This view with regard to the course of the fibres in the nerves is held by nearly all anatomists. Some, however, assert that branching and inosculation of individual fibres sometimes occur in the course of nerves;[2] but this statement is not sufficiently confirmed, in view of the very general opinion to the contrary. It has long been known, since the researches of Savi, Robin, Wagner, and others, that in the electric organs of certain fishes, the large nerve-fibres break up into numerous

[1] SAPPEY, *Recherches sur la structure de l'envelope fibreuse des nerfs.—Journal de l'anatomie*, Paris, 1868, tome v., p. 47, *et seq.*

[2] SCHULTZE, in STRICKER, *Handbuch der Lehre von den Geweben*, Leipzig, 1868, S. 119.

branches before they pass to their termination;[1] but there is no such arrangement in the human subject or in the higher animals, in the course of the nerves, or anywhere, except at the point where the fibres change their character just before their termination. The branching and inosculation of the ultimate nerve-fibres will be considered in connection with the very interesting and important question of their ultimate distribution to muscles and sensitive parts.

Mode of Termination of the Nerves in the Voluntary Muscles.—For a long time the actual mode of termination of the nerve-fibres in the muscles was a question of great uncertainty; but within the last few years, thanks to the elaborate researches of the French and German anatomists, the peripheral extremities of the nerves have been so accurately described and figured, that the great question of the mode of connection between the anatomical element conducting the stimulus to the muscles and the contractile elements of the muscles themselves may be considered as definitively settled. So many views, however, have been presented on this subject from time to time, that an historical account of the numerous researches, within even the last few years, would possess but little physiological interest.[2]

Before physiologists had any definite knowledge of the true mode of termination of the motor nerves, the only opinion on this subject entitled to any consideration was that of Prévost and Dumas, who believed that they had de-

[1] ROBIN, *Mémoire sur la démonstration expérimentale de la production d'électricité par un appareil propre aux poissons du genre des raies.—Journal de l'anatomie*, Paris, 1865, tome ii., p. 533, *et seq.*

[2] Prof. Trinchese, in an historical introduction to an account of his own observations on the peripheral termination of the nerves, gives an admirable review of recent researches on this subject. He is in error, however, in dating the view of the termination in loops from Valentin and Emmert, in 1836, this theory having been advanced by Prévost and Dumas, in 1823. (TRINCHESE, *Mémoire sur la terminaison périphérique des nerfs moteurs.—Journal de l'anatomie*, Paris, 1867, tome iv., p. 485, *et seq.*)

monstrated loops at the peripheral ends of the nerves resting on the muscular fibres. These loops were fully described and figured in 1823,[1] and this view was afterward quite generally adopted by physiologists; but it has been so completely overthrown by recent observations, that it is not now a question for discussion. In 1840, Doyère gave an account of the peripheral termination of the motor-nerves,[2] probably as accurate as was possible with his imperfect means of investigation; but, as is justly remarked by Prof. Trinchese, this observation, though confirmed a few years later by Quatrefages,[3] seems to have been lost sight of by most physiological writers.[4] In view of these early researches, it is unnecessary to consider elaborately the claims to priority of more recent observers, the results of whose investigations present slight and unimportant differences; and, although these have been brought forward and warmly discussed[5] as a matter of controversy, they possess but little interest.

We shall not enter into any further discussion of the views expressed by different anatomists with regard to the question under consideration, but will now simply describe the connection between the peripheral nerves and the muscles, as it appears from the researches that seem to be the most exact and reliable. Without underestimating the value of other researches, we may state that those of Rouget represent, perhaps, the present condition of the question as well as any. As we before remarked, the differences between the

[1] Prévost et Dumas, *Mémoire sur les phénomènes qui accompagnent la contraction de la fibre musculaire.—Journal de physiologie*, Paris, 1823, tome iii., p. 322.

[2] Doyère, *Mémoire sur les tardigrades.—Annales des sciences naturelles, Zoologie*, Paris, 1840, tome xiv., p. 346.

[3] Quatrefages, *Mémoire sur l'éolidine paradoxale.—Annales des sciences naturelles, Zoologie*, Paris, 1843, tome xix., p. 300.

[4] Trinchese (*loc. cit.*) alludes to the observations of Doyère, which are also fully discussed by Kühne (Stricker, *Handbuch der Lehre von den Geweben*, Leipzig, 1868, S. 147, *et seq.*).

[5] Beale, *An Anatomical Controversy. The Distribution of Nerves in Voluntary Muscle*, etc., London, 1865, pp. 38.

most reliable observations of recent writers are nearly all unimportant; and while future investigations may enable us to go further in following some of the elements of the nerve-fibres, they will, in all probability, simply extend our knowledge without invalidating the information already acquired.

The observations of Rouget were published in 1862, and were made upon lizards, frogs, Guinea-pigs, rats, and other animals, and confirmed in the human subject.[1] The tissues were taken either from the living animal or from an animal just killed, and were examined, in some instances, without the addition of reagents; but the most satisfactory results were obtained by macerating the muscles for from six to twenty-four hours in a liquid containing $\frac{1}{1000}$ of hydrochloric acid, and adding to the preparation on the glass slide a drop of a solution of sugar in water. In preparations made in this way, it is easy to trace the course of the nerves to their termination. The following is the description given by Rouget:

"The nervous trunks and the branches of distribution generally cross the course of the muscular fibres. As regards the terminal ramifications, sometimes they meet the muscular fibres at nearly a right angle, and sometimes they are placed nearly parallel to the axis of the primitive fasciculi. Branches of distribution are detached sometimes from branches containing two or three fibres, and sometimes from isolated fibres. After a very short course these tubes divide, and may present as many as seven or eight successive divisions. Most commonly, the termination takes place either by divisions of the second or third order, or the same tube gives off, successively, divisions which pass to the adjacent primitive fasciculi and terminate here without new divisions and after a very short course. They have a less diameter

[1] ROUGET, *Mémoire sur la terminaison des nerfs moteurs dans les muscles chez les reptiles, les oiseaux et les mammifères.—Journal de la physiologie*, Paris, 1862, tome v., p. 574, *et seq.*

than the primitive nerve-tubes, but they preserve even tc the terminal extremity their double contour, and there can be demonstrated, very easily, a sheath provided with nuclei, a medullary layer, and the *axis-cylinder*. Never do we observe at the termination of the motor nerves the pale and non-medullated fibres described by Kühne and Kölliker. At the point where the tube terminates, we remark constantly a special arrangement which has no analogy with that which has been described in the batrachia by these two observers, and which Kühne believed could be extended to the higher vertebrata, to the mammalia, and to the human subject. The nerve-tube, with a double contour, preserving still a diameter of from $\frac{1}{3000}$ to $\frac{1}{2500}$ of an inch at the point where it touches the primitive fasciculus to become arrested at its surface, terminates by an expansion of the central nerve-substance, the axis-cylinder, which is in immediate contact with the contractile fibres (fibrillæ) of the primitive fasciculus. The layer of medullary substance ceases abruptly at this point, the sheath of the tube is spread out and blended with the sarcolemma; but in immediate continuity with the axis-cylinder, a layer, a plate of granular substance, from $\frac{1}{6000}$ to $\frac{1}{4000}$ of an inch in thickness, is spread out beneath the sarcolemma, on the surface of the fibrillæ, in a space generally oval and about $\frac{1}{1250}$ of an inch wide in its short diameter, and $\frac{1}{500}$ of an inch in its long diameter. This granular substance masks more or less completely, in the space which corresponds to it, the transverse striæ of the muscular fasciculus. The disk itself has exactly the granular appearance of the substance of the axis-cylinder in the vertebrata, and of that of the nerve-tubes in most of the invertebrata, especially after being treated by diluted acids. But that which essentially characterizes the terminal plates of the motor nerves is an agglomeration of nuclei observed at their site. With a low magnifying power, even, we can distinguish the point where a nerve-tube touches the primitive fasciculus to which it belongs, and ends abruptly at its

surface, by a collection of from six to twelve or even sixteen nuclei which occupy the site of the terminal plate. These nuclei are distinguished by their size as well as by their form, which is less elongated than the nuclei of the muscular tissue (*connective-tissue nuclei of the primitive fasciculi*). They present, however, the most complete analogy with the nuclei of the nerve-sheath (*connective-tissue nuclei of the nerves*). They are, without any doubt, nothing else than the nuclei which, scattered throughout the entire length of the sheath, are collected in a mass at the point where the covering of the nerve-fibre is spread out and fuses with the sarcolemma of the primitive fasciculus."

There can be little if any doubt that the description just given represents the mode of termination of the nerves in the voluntary muscles in man and the mammalia. The observations of Kölliker,[1] who describes a plexus of pale fibres with nuclei instead of a well-defined terminal plate, were made upon frogs, and are probably correct; and Kölliker admits the accuracy of the observations of Rouget as regards reptiles, birds, and the mammalia.[2] The views of Beale[3] are only entitled to consideration in so far as they confirm previous observations. His descriptions and figures, as far as we know, are not accepted, nor have they been confirmed by any anatomist who has investigated the subject. The appearances of the terminal plates are represented in Fig. 3.

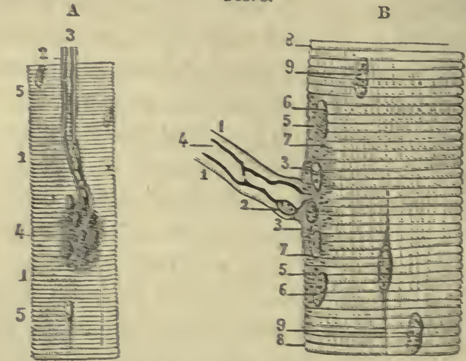
Although the sensibility of the muscles is slight as compared with that of the tegumentary tissues, they undoubtedly possess nerve-fibres other than those exclusively devoted to motion. In addition to the fibres just described, Kölliker and some others have noted fibres with a different mode of termination. These Kölliker believes to be sensitive nerves, and their mode of termination has not been so definitely described as in the fibres with terminal motor plates. We refrain from giving a very full description even of what has

[1] KÖLLIKER, *Éléments d'histologie humaine*, Paris, 1868, p. 222, *et seq.*

[2] KÖLLIKER, *op. cit.*, p. 225. [3] *Loc. cit.*

been observed with regard to the termination of these fibres, for future and more successful researches will probably modify the views now held with regard to this point. Kölliker[1] states that the fibres in question are very fine, dark-bordered tubes, with a medullated sheath, which, when studied in

Fig. 8.



Mode of termination of the motor nerves, after Rouget.

A. Primitive fasciculus of the thyro-hyoid muscle of the human subject, and its nerve-tube.—1, 1, primitive muscular fasciculus; 2, nerve-tube; 3, medullary substance of the tube, which is seen extending to the terminal plate, where it disappears; 4, terminal plate situated *beneath* the sarcolemma, that is to say, between it and the elementary fibrillæ; 5, 5, sarcolemma.
B. Primitive fasciculus of the intercostal muscle of the lizard, in which a nerve-tube terminates.—1, 1, sheath of the nerve-tube; 2, nucleus of the sheath; 3, 3, sarcolemma becoming continuous with the sheath; 4, medullary substance of the nerve-tube ceasing abruptly at the site of the terminal plate; 5, 5, terminal plate; 6, 6, nuclei of the plate; 7, 7, granular substance which forms the principal element of the terminal plate, and which is continuous with the axis-cylinder; 8, 8, undulations of the sarcolemma reproducing those of the fibrillæ; 9, 9, nuclei of the sarcolemma. (Longet, *Traité de Physiologie*, Paris, 1869, tome iii., p. 99.)

muscular tissue rendered pale by acetic acid, may be seen to give off exceedingly fine, non-medullated fibres, which terminate in fibres of the same appearance, but provided with nuclei. It does not appear to be certain how these fibres end. Kölliker is not satisfied that the free extremities, as they appear to be, are the actual terminations; but he asserts that in some rare instances they communicate with each other. For the present this point must be considered as unsettled.

Mode of Termination of the Nerves in the Involuntary Muscular Tissue.—The nerves have not been followed out

[1] Kölliker, *op. cit.*, p. 228.

so satisfactorily in the involuntary as in the striated muscular system; and as most, if not all of the fibres are derived from the sympathetic system, which contains numerous fibres of Remak the terminations of which have not been described, it is evident that our information concerning this part of the peripheral nervous system must be incomplete. Perhaps the most remarkable of the late observations upon this point are those of Dr. Frankenhaeuser, upon the nerves of the uterus. These researches were very elaborate; but the point most interesting in this connection is that the nerves, having formed a plexus in the connective tissue, send exceedingly small fibres into the sheets or layers of muscular-fibre cells, which branch and finally go into the nucleoli of these structures.[1] Arnold has confirmed these observations, and has shown farther that in many instances the fine terminal nerve-fibres branch and go into the nuclei of the muscular fibres, and then pass out to join with other fibres and form a plexus.[2]

Termination of the Nerves in Glands.—The great influence which the nervous system exerts upon secretion attaches considerable interest to recent researches into the ultimate distribution of the nerves in the glands. It must be remembered, however, in these, as in all observations upon the destination of the smallest nerve-fibres, that the problem is one of the most difficult in the whole range of minute anatomy; and the results arrived at must be received

[1] FRANKENHAEUSER, *Die Nerven der Gebaermutter und ihre Endigung in den glatten Muskel-fasern*, Jena, 1867, S. 76, Taf. viii.

[2] ARNOLD, in STRICKER, *Manual of Human and Comparative Histology*, London, 1870, vol. i., p. 195, *et seq.* The exact mode of termination of the nerves in the organic muscles cannot be regarded as definitively settled. We have attempted, however, to give what seem to be the most reliable views on this subject, deduced from recent observations. For a further discussion of some of the points which we have accepted as probable, the reader is referred to a recent article by Krause. (*Die Nervenendigung in den glatten Muskeln.—Archiv für Anatomie, Physiologie und wissenschaftliche Medicin*, Leipzig, 1870, S. 1, *et seq.*)

with a certain amount of caution, until they shall have been amply confirmed.

The researches of Pflüger upon the salivary glands leave no doubt as to the fact that medullated nerve-fibres pass to the cells of these organs and there abruptly terminate, at least as dark-bordered fibres. This author believes, however, that, having formed a more or less branching plexus, non-medullated fibres pass directly into the glandular cells, and he gives figures which seem to illustrate this arrangement pretty clearly. The same observer describes and figures multipolar cells, mixed with the glandular cells, in which some of the nerve-fibres terminate.[1]

Modes of Termination of the Sensory Nerves.—There are undoubtedly several modes of termination of the sensitive nerves in integument and mucous membranes, some of which have been accurately enough described, while others are still somewhat uncertain. In the first place, anatomists now recognize three varieties of corpuscular terminations, differing in their structure, probably, according to the different functions connected with sensation, with which the parts are endowed. In addition, it is probable that many sensitive nerves are connected with the hair-follicles, which are so largely distributed throughout the cutaneous surface. There are, also, terminal filaments not connected with any special organs, some of them, perhaps, ending simply in free extremities, and some connected with epithelium. There is still considerable difference of opinion among anatomists

[1] PFLÜGER, in STRICKER, *Manual of Human and Comparative Histology*, London, 1870, vol. i., p. 433, *et seq.* The views here advanced by Pflüger have been confirmed by him in more recent observations and extended to the pancreas (*Journal of Anatomy and Physiology*, Cambridge and London, 1870, vol. iv., p. 156). Pflüger states, also, his belief that the same connection exists between the nerves and the liver-cells (ibid., p. 188). The question, however, is still somewhat uncertain, and Mayer, in examinations of the salivary glands, found filaments in connection with the nuclei, but failed to satisfy himself that they were nervous (*Quarterly Journal of Microscopical Science*, London, April, 1870, p. 199)

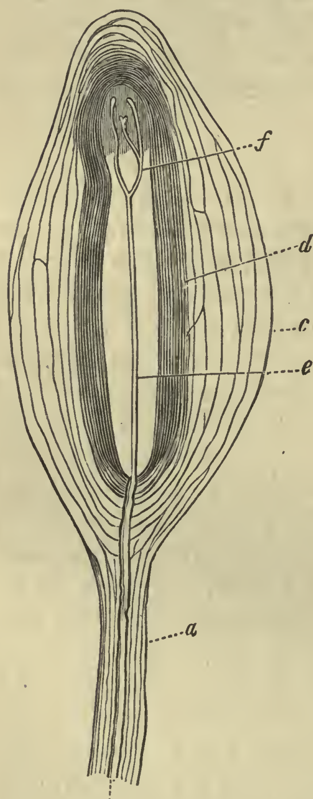
concerning all of these various points, but with regard to the terminal corpuscles, these differences are purely anatomical, and do not materially affect the physiology of sensation. We do not propose, therefore, to enter fully into the discussions upon these questions, and will simply present what seem to be the most reasonable views of the latest and most reliable observers.

Corpuscles of Pacini, or of Vater.—These corpuscles, which were the first discovered and described in connection with the sensitive nerves, were called corpuscles of Pacini, until it was shown that they had been seen about a century and a half ago by Vater. Their actual mode of connection with the nerves, however, has only been ascertained within the last few years. The following are the measurements of these bodies and the situations in which they are found, taken from Kölliker:[1]

In man, these corpuscles are oval or egg-shaped, and measure from $\frac{1}{20}$ to $\frac{1}{6}$ of an inch in length. They are always found in the subcutaneous layer on the palms of the hands and the soles of the feet, and are most numerous on the palmar surfaces of the fingers and toes, particularly the third phalanges. In the entire hand there are about six hundred, and about the same on the feet. They are sometimes, but not constantly, found in the following situations: The dorsal surfaces of the hands and feet; on the cutaneous nerves of the arm, the forearm and the neck, the internal pudic nerve, the intercostal nerves, all of the articular nerves of the extremities, the nerves beneath the mammary glands, the nerves of the nipples, and in the substance of the muscles of the hands and feet. They are found without exception on all of the great plexuses of the sympathetic system, in front of and by the sides of the abdominal aorta, and behind the peritoneum, particularly in the vicinity of the

[1] KÖLLIKER, *Éléments d'histologie humaine*, Paris, 1868, p. 141.

pancreas. They sometimes exist in the mesentery, and have been observed near the coccygeal gland.



Pacinian corpuscle from the human subject, magnified 350 diameters.—*a*, pedicle of the corpuscle; *b*, nerve-fibre contained in its interior; *c*, external layer of its covering; *d*, internal layer; *e*, pale nerve-fibre within the internal transparent bulb; *f*, divisions and extremities of the fibre. (KÖLLIKER, *Handbuch der Gewebelehre*, Leipzig, 1867, S. 108.)

The structure of the corpuscles consists simply of several layers of connective tissue enclosing a central bulb in which is found the terminal extremity of the nerve. This bulb is finely granular, nucleated, and is considered by most anatomists to be composed of connective tissue. At the base of the corpuscle is a pedicle formed of connective tissue surrounding a medullated nerve-fibre which penetrates the corpuscle and terminates in the central bulb.

The only really important point of discussion with reference to the structure of the nerve-fibre in the central bulb, and this is purely anatomical, is whether or not the medullary substance extends into the corpuscle itself. Probably the fibre is here reduced simply to the axis-cylinder. Kölliker thinks that there is a very thin layer of medullary substance, but he states that this is a question difficult to decide.[1] All anatomists agree that a single thin, flat fibre penetrates the corpuscle and terminates near its summit in two or three branches, with slightly enlarged

[1] *Op. cit.*, p. 143.

and granular extremities. The arrangement of the different anatomical elements is shown in Fig. 4.

The situation of these corpuscles beneath, instead of in the substance of the true skin, shows that they cannot be properly considered as tactile corpuscles, a name which is applied to other structures situated in the papillæ of the corium; and it is impossible to assign to them any special function connected with sensation, such as the sense of temperature, or the appreciation of pressure or weight. All that we can say with regard to them is that they constitute one of the several modes of termination of the nerves of general sensibility.

Tactile Corpuscles.—The name tactile corpuscles implies that these bodies are connected with the sense of touch; and this view is sustained by the fact that they are found almost exclusively in parts endowed to a marked degree with tactile sensibility. They are sometimes called the corpuscles of Meissner and Wagner, after the anatomists by whom they were first described. The most interesting researches into their structure, however, are of later date. The view ordinarily accepted with regard to the structure of these bodies is that adopted by Kölliker, who has himself investigated their anatomy very closely; but his researches have been controverted very strongly by Rouget. All are agreed concerning the situations where these corpuscles are found, their number, etc., the discussions with regard to their structure being confined to their mode of connection with the nerve-fibres.

The true tactile corpuscles are found in greatest number on the palmar surfaces of the hands and fingers and the plantar surfaces of the feet and toes. They exist, also, in the skin on the backs of the hands and feet, the nipples, and a few on the anterior surface of the forearm. As we shall see when we come to describe them fully, they are situated in the substance of the papillæ of the skin, and they cannot fail

to have an important function in connection with the sense of touch.

We have already treated of the structure of the skin in another volume,[1] where we have seen that the largest papillæ, measuring from $\frac{1}{250}$ to $\frac{1}{200}$ of an inch in length, are found on the hands, feet, and nipples, precisely where the tactile corpuscles are most abundant. Corpuscles do not exist in all papillæ, and are found chiefly in those called compound. In the space of about $\frac{1}{50}$ of an inch square on the third phalanx of the index-finger, Meissner counted four hundred papillæ, in one hundred and eight of which he found tactile corpuscles, or about one in four. In the same space on the second phalanx, he found forty corpuscles; on the first phalanx, fifteen; eight on the skin of the hypothenar eminence; thirty-four on the plantar surface of the ungual phalanx of the great-toe; and seven or eight in the skin on the middle of the sole of the foot. In the skin of the forearm, the corpuscles are very rare.[2] Kölliker states, also, that the tactile corpuscles usually occupy special papillæ, which are not provided with blood-vessels; so that the papillæ of the hand may be properly divided into vascular and nervous.

The form of the tactile corpuscles is oblong, with their long diameter in the direction of the papillæ. Their length is from $\frac{1}{380}$ to $\frac{1}{225}$ of an inch. In the palm of the hand, they are from $\frac{1}{225}$ to $\frac{1}{140}$ of an inch long, and from $\frac{1}{550}$ to $\frac{1}{500}$ of an inch in thickness.[3] They are generally situated at the summits of the secondary eminences of the compound papillæ.

It is almost certain that the tactile corpuscles consist of connective-tissue elements, with nerve-fibres making a few spiral turns on their surface and finally disappearing in their substance. This view is most ably supported by Kölliker, in opposition to the proposition advanced by Rouget, that the

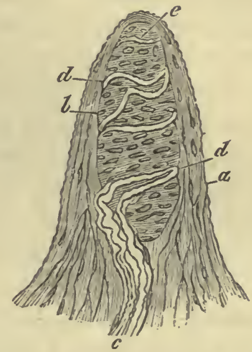
[1] See vol. iii., Excretion, p. 115.

[2] Kölliker, *Éléments d'histologie humaine*, Paris, 1868, p. 139.

[3] Kölliker, *op. cit.*, p. 138.

striæ on the surface of the corpuscles are produced exclusively by nerve-fibres. According to Kölliker, the tactile corpuscles consist of a central bulb of homogeneous or slightly granular connective-tissue substance, analogous to the central bulb of the Pacinian corpuscles, and a covering. Treated with acetic acid, the covering presents numerous elongated nuclei arranged in a circular manner, which he believes to be nuclei of connective tissue, and a few fine elastic fibres. One, two, and sometimes three or four dark-bordered nerve-fibres pass from the subcutaneous nervous plexus to the base of each corpuscle. These surround the corpuscle with two or three spiral turns, and terminate by pale extremities at the surface of the central bulb.[1] This arrangement is shown in Fig. 5.

Fig. 5.



Cutaneous papilla.—*a*, cortical layer with plasmatic cells and fine elastic fibres; *b*, tactile corpuscle, with transverse nuclei; *c*, afferent nervous branch, with its nucleated neurilemma; *d*, nerve-fibres encircling the corpuscle; *e*, the apparent termination of one of these fibres. (Kölliker, *Handbuch der Gewebelehre*, Leipzig, 1867, S. 106.)

Rouget believes that the spiral lines on the surface of the corpuscles are produced exclusively by gelatinous, nucleated nerve-fibres which cover them completely, sometimes dividing and sometimes remaining single, and that the fibres terminate in a nucleated central mass, entirely analogous to the nucleated expansion of the motor nerves. He claims to have demonstrated this in preparations treated for two or three days in a liquid containing one drop of acetic acid in about three and a third fluidounces of water, and afterward washed in pure water, which denudes the papillæ of their epithelium.[2] In his endeavor to establish a

[1] Kölliker, *op. cit.*, p. 138.

[2] Rouget, *Mémoire sur les corpuscles nerveux qui se rencontrent à l'origine des nerfs sensitifs, dans les papilles de la peau et des muqueuses.—Archives de physiologie*, Paris, 1868, tome i., p. 599.

complete analogy between the terminations of the sensitive and the motor nerve-fibres, Rouget does not seem to be entirely sustained; for the behavior of the different anatomical elements of the tactile corpuscles when treated by acetic acid, and again when colored with carmine, shows conclusively the presence of connective-tissue elements in their outer covering. The observations of Kölliker and others leave no doubt upon this point;[1] and as we have already seen in treating of the structure of the nerve-fibres,[2] the changes produced by acetic acid enable us to readily distinguish the gelatinous nucleated fibres from the elements of connective tissue. While the exact mode of termination of the fibres in the tactile corpuscles is not perfectly clear, we must adopt for the present the views of Kölliker, as the most reasonable and satisfactory.

Terminal Bulbs.—Under this name, a variety of corpuscles has lately been described by Krause[3] as existing in the conjunctiva covering the eye and in the semilunar fold, the floor of the buccal cavity, the tongue, the glans penis, and the clitoris. They bear some analogy to the tactile corpuscles, but are much smaller and more simple in their structure. They form simply a rounded or oblong enlargement at the ends of the nerves, which is composed of homogeneous matter with an exceedingly delicate investment of connective tissue. They measure from $\frac{1}{1000}$ to $\frac{1}{250}$ of an inch in diameter. In the parts provided with papillæ, they are situated at the summits of the secondary elevations.

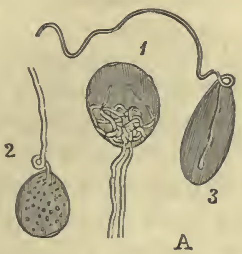
The arrangement of the nerve-fibres in these corpuscles is very simple. One, two, or three medullated fibres pass from the submucous plexus to the corpuscles. The investing sheath of the fibres is here continuous with the connective-tissue covering of the corpuscle, and the nerve-

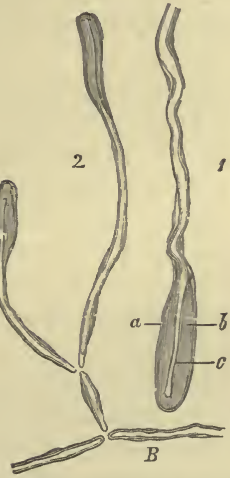
[1] *Loc. cit.* [2] See page 26.

[3] W. Krause, *Die terminalen Körperchen der einfach sensibilen Nerven*, Hannover, 1860, S. 125, *et seq.*

fibres pass into the corpuscle, break up into two or three divisions, and terminate in convoluted or knotted coils.

FIG. 6.





A. Three corpuscles of Krause from the conjunctiva of man, treated with acetic acid (magnified 300 diameters); after a drawing by Lüdden.—1, spherical corpuscle, with two nerve-fibres which form a knot in its interior. Portions of two pale nerve-fibres are also seen. 2, a rounded corpuscle presenting a nerve-fibre and fatty granulations in the internal bulb; 3, an elongated corpuscle with a distinct terminal fibre. In these three corpuscles, the covering, nucleated in 1 and 2, is distinguished.

B. Terminal bulbs from the conjunctiva of the calf, treated with acetic acid (magnified 300 diameters); after a drawing by Lüdden.—1, extremity of a nerve-fibre with its bulb; 2, double bifurcation of a nerve-fibre, with two terminal bulbs; *a*, covering of the terminal bulbs; *b*, internal bulb; *c*, pale nerve-fibre. (KÖLLIKER, *Handbuch der Gewebelehre*, Leipzig, 1867, S. 103.)

The nerve-fibres are medullated for a certain distance, but their terminations are generally pale. The above is one

form of these corpuscles. Sometimes, however, the terminal bulbs are oblong, and sometimes but a single nerve-fibre penetrates the bulb and terminates in a simple pale filament. The principal forms of the terminal bulbs are shown in Fig. 6.

General Mode of Termination of the Sensory Nerves.—The actual termination of the sensitive nerves upon the general surface and in mucous membranes is still a question of great obscurity. Though we have arrived at a pretty definite knowledge of the sensitive corpuscles, it must be remembered that there is an immense cutaneous and mucous surface in which no corpuscles have as yet been demonstrated; and it is in these parts, endowed with what we may call general sensibility, as distinguished from the sense of touch, that we have to study the mode of termination of the nerves.

Kölliker is of the opinion that, in the immense majority of instances, the sensitive nerves terminate in some way in the hair-follicles.[1] If this be true, it will account for the termination of the nerves in by far the greatest portion of the skin, as there are few parts in which hair-follicles do not exist; but, unfortunately, the exact mode of connection of the nerves with these follicles is not apparent. The following is all we know positively of the terminations of the nerves on the general surface:

Medullated nerve-fibres form a plexus in the deeper layers of the true skin, from which fibres, some pale and nucleated and others medullated, pass to the hair-follicles, divide into branches, penetrate into their interior, and are there lost. A certain number of fibres pass to the non-striated muscular fibres of the skin. A certain number pass to papillæ and terminate in tactile corpuscles, and others pass to papillæ that have no tactile corpuscles.

In the mucous membranes, as far as we know, the mode of termination is, in general terms, by a delicate plexus just

[1] *Op. cit.*, p. 144.

beneath the epithelium, coming from a submucous plexus analogous to the deep cutaneous plexus. In certain membranes, we have already noted the termination in bulbs (corpuscles of Krause). In the cornea the fibres have been followed more minutely than in any other situation, and the results of recent researches on this subject are very remarkable. These results are so recent and unexpected, that we are hardly prepared to admit them unreservedly without fuller confirmation. At present we can only state that the observations of Hoyer,[1] Lipmann,[2] and others, confirmed in part by Kölliker,[3] seem to show that branching nerve-fibres pass to the nucleoli of the corpuscles of the cornea and to the nucleoli of the cells of the posterior layer of epithelium.

Structure of the Nerve-centres.

A peculiar pigmentary matter in the nerve-cells and the surrounding granular substance gives to the nerve-centres a grayish color, by which they are readily distinguished from the white, or fibrous division of the nervous system. Wherever this gray matter is found, the anatomical elements of the tissue are cellular, except in the nerves formed of gray, or gelatinous fibres. Under the general division of nerve-centres, we include, anatomically at least, the gray matter of the cerebro-spinal centres, the ganglia of the roots of the spinal and certain of the cranial nerves, and the numerous ganglia of the sympathetic system. In these parts are found cells, which constitute the essential anatomical element of the tissue, granular matter resembling the contents of the cells, pale fibres originating in prolongations of the cells, elements of connective tissue, delicate membranes

[1] HOYER, *Ueber den Anstritt von Nervenfaser in das Epithel der Hornhaut.—Archiv für Anatomie, Physiologie und wissenschaftliche Medicin*, Leipzig, 1866, S. 180, *et seq.*

[2] LIPPMANN, *Ueber die Endigung den Nerven im eigentlichen Gewebe und im hinteren Epithel der Hornhaut des Frosches.—Archiv für Pathologie, Anatomie und Physiologie*, Berlin, 1869, Bd. xlviii., S. 218, *et seq.*

[3] KÖLLIKER, *Éléments d'histologie humaine*, Paris, 1868, p. 145.

enveloping some of the cells, and vessels. The most interesting and important of these structures, in their physiological relations, are the cells and the prolongations by which they are connected with the nerves.

Nerve-cells.—Anatomists are now pretty well agreed that the following varieties of cells exist in the nerve-centres, and constitute their essential anatomical elements; viz., apolar, unipolar, bipolar, and multipolar cells. Although some have denied the existence of apolar cells, there can be little doubt of their presence in the centres in small numbers, and, as is suggested by Kölliker, they may be nerve-cells in an imperfect state of development. The nerve-cells present great differences in their size and general appearance, and some distinct varieties are found in particular portions of the nervous system, and are probably connected with special functions.

The apolar cells are simply rounded bodies, with granular contents, a nucleus and nucleolus like other cells, but without any prolongations connecting them with the nerve-fibres. They have been observed in the cerebro-spinal centres, and they always exist in the sympathetic ganglia. Those who deny their existence believe that the poles have been detached in preparing specimens for examination. Unipolar cells exist in some of the lower orders of animals, but their presence in the human subject is doubtful. Bipolar cells are found in the ganglia of the posterior roots of the spinal nerves, where they are of considerable size. Smaller bipolar cells are found in the sympathetic ganglia. Multipolar cells present three or more prolongations.

Small cells, with three, and rarely four prolongations, are found in the posterior cornua of the gray matter of the spinal cord. From their situation they have been called sensitive cells. They are undoubtedly found in greatest number in parts known to be endowed exclusively with sensitive properties.

Large, irregularly-shaped multipolar cells, with numerous prolongations, are found chiefly in the anterior cornua of the gray matter of the spinal cord, and have been called motor cells. These sometimes present as many as ten or twelve poles.

With all these differences in the size and form of the nerve-cells, they present tolerably uniform general characters as regards their structure and contents. Leaving out the apolar and unipolar cells, the perfectly-developed cells are of an exceedingly irregular shape, with strongly-refracting, granular contents, frequently a considerable number of pigmentary granules, and a distinct nucleus and nucleolus. The nucleus in the adult is almost invariably single, though, in very rare instances, two have been observed. Cells with multiple nuclei are often observed in young animals. The nucleoli are usually single, but there may be as many as four or five. The strongly-refracting contents, the peculiar shape, and the poles or prolongations give the nerve-cells an exceedingly characteristic appearance, which is represented in Fig. 7.

The diameter of the cells is as variable as their form. They usually measure from $\frac{1}{1250}$ to $\frac{1}{500}$ of an inch;[1] but there are many of larger size, and some are smaller. The nuclei measure from $\frac{1}{2000}$ to $\frac{1}{1250}$ of an inch.

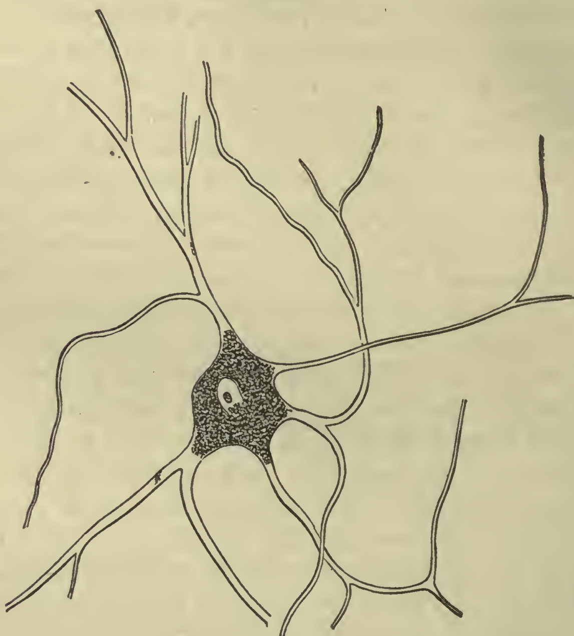
The nerve-cells are so delicate and prone to alteration that their study is exceedingly difficult. Sections of the nerve-centres must be prepared with great care, and are not easily made and preserved. In the numerous anatomical investigations that have been made within the last few years, the centres have generally been hardened artificially; and almost every investigator has used different processes and reagents, which may account in a measure for the differences of opinion that now exist on all points connected with the minute anatomy of these parts.

There is at the present time considerable discussion with

[1] POUCHET, *Précis d'histologie humaine*, Paris, 1864, p. 139.

regard to the intimate structure of the substance of the nerve-cells, their nuclei and nucleoli, and the points involved have a certain amount of physiological interest. In the first place, the transverse striæ in the axis-cylinder treated with nitrate of silver, noted by Frommann and confirmed by Grandry and others, have been observed by Grandry in the substance of the nerve-cells.[1] While this fact, perhaps, shows that the

FIG. 7.



Nerve-cell from the ferruginous substance which forms the floor of the rhomboidal sinus, in man. Magnified 850 diameters. (KÖLLIKER, *Handbuch der Gewebelehre*, Leipzig, 1867, S. 291.)

substance contained in the cells and their prolongations is the same as the substance of the axis-cylinder, as we stated with regard to the axis-cylinder, it is possible that the mark-

[1] See page 22.

ings may be entirely artificial, and that they do not demonstrate the existence of two distinct substances in the tissue.

The most interesting question with regard to the structure of the nerve-cells relates to the mode of origin of their fibres, or poles. Until quite recently these have been regarded as simple prolongations of the substance of the cells; but lately the view has been advanced that the nerve-cells, in the human subject, are composed of regular fibrils continuous with the poles and starting, as it were, from the nucleoli.[1] The fibrillation of the nerve-cells and their prolongations is figured by Schultze in an article in one of the most authoritative of the recent works on histology;[2] but some other eminent observers have failed to note the appearances here described,[3] at least in the human subject and the mammalia. With our present knowledge of the physiology of the nerve-cells, the question whether or not their substance be fibrillated has little more than an anatomical interest; but there can be no doubt that the cells of some of the lower orders of animals possess striations more or less regular. These, indeed, were described soon after the cells were discovered. While there is no anatomist who denies the fact that the substance of the cells is marked by striæ in many animals, the existence of an analogous arrangement in the human subject is still doubtful. Some anatomists, with Schultze, admit the striations, but have failed to connect them with the nuclei and nucleoli. All admit that they are demonstrated with great difficulty; and,

[1] Beale, *Indications of the Paths taken by the Nerve-currents as they traverse the caudate Nerve-cells of the Spinal Cord and Encephalon.—Proceedings of the Royal Society*, London, 1864, vol. xiii., p. 386, *et seq.*

——— Frommann, *Ueber die Färbung der Binde- und Nervensubstanz des Rückenmarkes durch Argentum nitricum und über die Struktur der Nervenzellen.—Archiv für pathologische Anatomie und Physiologie*, Berlin, 1864, Bd. xxxi., S. 134.

[2] Schultze, in Stricker, *Manual of Human and Comparative Histology*, London, 1870, vol. i., p. 179.

[3] Kölliker, *Éléments d'histologie humaine*, Paris, 1868, p. 332.

while this question is so important that it can hardly be neglected in studying the physiological anatomy of the nerve-centres, it is one concerning which it seems impossible to express a positive and definite opinion.

Connection of the Nerve-cells with the Fibres and with each other.—Although the mode of connection of the nerve-cells with the fibres and with each other is one of the most important, in its physiological bearings, of all the points connected with the minute anatomy of the nerve-centres, it is impossible, in the present state of our anatomical knowledge, to answer the questions involved in a manner entirely satisfactory. This statement is made after a thorough study of the investigations of the most reliable modern observers, among whom may be mentioned Stilling, Lockhart Clarke, Kölliker, R. Wagner, Jacubowitsch, Van der Kolk, Deiters, J. Dean, and Schultze, as the most prominent, with many others who have investigated the subject more or less successfully.[1] A full discussion of the different opinions and the methods of investigation that have been employed would be out of place in this work. The difficulties in the way of arriving at positive information upon these questions are the following:

1. The nerve-cells and their prolongations are so delicate and easily torn that they cannot be isolated and followed for any considerable distance, and theoretical considerations are constantly required to fill up the deficiencies in actual observation.

2. In the study of sections of the nerve-centres, the parts must be hardened and afterward rendered transparent by reagents, which must produce more or less change in the structures; and it seems an anatomical impossibility to make these sections so as to follow out the prolongations of the

[1] Kölliker gives a very full bibliography of the anatomy of the nervous system, to which the reader is referred for more extended information. (*Éléments d'histologie humaine*, Paris, 1868, p. 441.)

cells far enough to establish beyond doubt their exact relations.

These two considerations alone are sufficient to account for the uncertainty so apparent even in the most successful investigations into the anatomy of the central nervous system; and we shall content ourselves, in view of these facts, with giving a summary of what seems to be the probable relation of the cells to the fibres of origin of the nerves and to each other.

Apolar cells, if they exist at all and be not cells from which the poles have become separated, are simple, rounded bodies, lying between the fibres, with which they have no other relation than that of mere contiguity. Unipolar cells have but one prolongation, which is continuous with a nerve-fibre. It is not certain that these exist in the human subject.

Bipolar cells are found in the ganglia of the posterior roots of the spinal nerves and some of the sympathetic ganglia. In many of the lower animals, particularly in fishes, the cells of the ganglia of the spinal nerves are simple, nucleated enlargements in the course of the sensitive nerve-fibres; and many anatomists have inferred that the same arrangement exists in man and the mammalia;[1] but the constitution of these ganglia in the higher classes of animals seems to be entirely different. In the first place, the roots of the spinal nerves at the ganglia are undoubtedly reënforced by the addition of new fibres, as Kölliker has shown by actual measurement, the roots being sensibly larger beyond the ganglia while the filaments of entrance and exit have the same diameter.[2] Direct observation upon the ganglia in man also fails to show the arrangement so clearly demonstrable in fishes. The cells in the posterior roots are not continuous with the fibres passing from the periphery to the cord, but give origin to new fibres, generally two in number, which sometimes are

[1] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 95.

[2] KÖLLIKER, *Éléments d'histologie humaine*, Paris, 1868, p. 419.

single and sometimes bifurcated, and which pass, in by far the greatest number if not in all instances, to the periphery.

The multipolar cells, with three or more prolongations, are found in all of the ganglia, but they predominate largely in the gray matter of the cerebro-spinal centres. It is the question of the exact mode of connection between these cells and the fibres of origin of the cerebro-spinal nerves and the union of the cells with each other by commissural prolongations, that presents the greatest difficulty and uncertainty. One point, which has been raised within a few years, is with regard to the character of the different poles connected with the same cell. In ordinary preparations of the central nervous system, it is impossible, even with the highest available magnifying powers, to distinguish any one pole which, in its general characters and connections, is different from the others; yet, some of the anatomists to whose researches we have alluded describe a single pole, more distinct in its outlines than the others, which does not branch and is to be regarded as an axis-cylinder. The other poles are supposed to be of a different character, not connected with the nerve-fibres, and always presenting a greater or less number of branches. These views are accepted by Schultze, who gives a figure, after Deiters, in which the contrast between the poles is represented as very marked;[1] but although this opinion is accepted by other high authorities,[2] it is not easy to understand how it can be received without reserve, when it is so difficult, if not impossible, to follow out the poles, except for a very short distance.

With our present means of investigation, there seems to be no doubt with regard to the following facts: Tracing the nerve-fibres toward their origin, they are seen to lose their investing membrane as soon as they pass into the white portion of the centres, being here composed only

[1] STRICKER, *Manual of Human and Comparative Histology*, London, 1870, vol. i., p. 177.

[2] KÖLLIKER, *Éléments d'histologie humaine*, Paris, 1868, p. 362

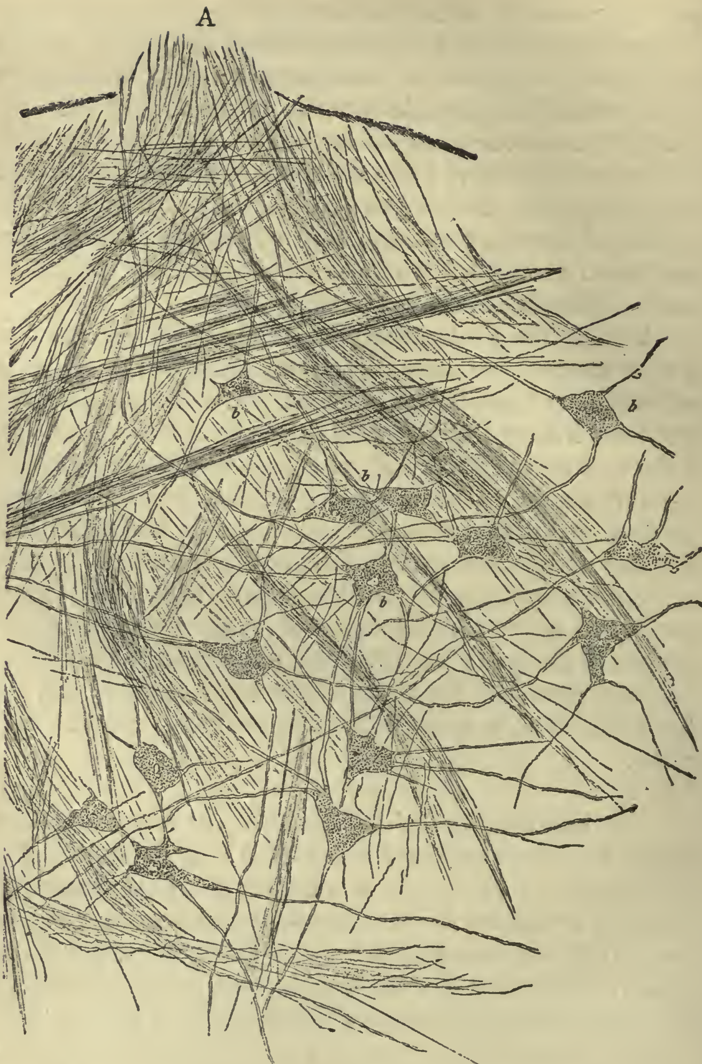
of the medullary substance surrounding the axis-cylinder. They then penetrate the gray substance, in the form of axis-cylinders, losing here the medullary substance. In the gray substance, it is impossible to make out of all their relations distinctly, and we cannot assume, as a matter of positive demonstration, that all of them are connected with the poles of the nerve-cells. Still, it has been shown, in the gray matter of the spinal cord, that many of the fibres are actual prolongations of the cells, the others probably passing upward to be connected with cells in the encephalon.

Tracing the prolongations from the cells, we find that one or more of the poles branch and subdivide in the gray substance, and give origin to fibres, but that these fibres do not branch after they pass into the white substance. Other poles connect the nerve-cells with each other by commissural fibres of greater or less length; but it has never been positively demonstrated that the cells are thus connected into separate and distinct groups, though this is possible.

The accompanying figure, taken from the excellent monograph on the lumbar enlargement of the spinal cord, by Dean, shows the mode of connection between certain of the cellular prolongations and the fibres of the anterior roots, and the commissural fibres by which the cells are connected with each other.

Accessory Anatomical Elements in the Nerve-centres.—While we must regard the cells of the gray matter and the axis-cylinder of the nerves as probably the only anatomical elements concerned in innervation, there are other structures in the nervous system which it is important for us to study. These are: 1, outer coverings surrounding some of the cells; 2, intercellular, granular matter; 3, peculiar corpuscles, called myelocytes; 4, connective-tissue elements; 5, blood-vessels and lymphatics.

Certain of the cells in the spinal ganglia and the ganglia of the sympathetic system are surrounded with a nucleated



Group of cells connected with the anterior roots, as seen in a transverse section, from the anterior cornu of the sheep.—*A*, entrance of the anterior roots into the cornu; *b*, *b*, *b*, *b*, cells connected by long, slender processes, with the anterior roots; *c*, boundary of the cornu. In this figure almost every variety of cell-connection may be seen, with bundles of fibres crossing in every direction. (DEAN, ***Microscopic Anatomy of the Lumbar Enlargement of the Spinal Cord***, Cambridge, 1861, Fig. 4.)

covering, some distance removed from the cell itself so as to be nearly twice the diameter of the cell, which is continuous with the sheath of the dark-bordered fibres.[1] This membrane is always nucleated, and Kölliker has lately shown that it is not homogeneous, as was at one time supposed, but is composed of a layer of very delicate epithelium.[2] The physiological significance of this covering is not apparent.

In the gray matter of the nerve-centres, there is a finely-granular substance between the cells, which closely resembles the granular contents of the cells themselves. In addition to this granular matter, Robin has described new anatomical elements which he has called myelocytes. These are found in the cerebro-spinal centres, forming a layer near the boundary of the white substance, and are particularly abundant in the cerebellum. They exist in the form of free nuclei and nucleated cells, the free nuclei being by far the more numerous. The nuclei are rounded or ovoid, with strongly-accentuated borders, are unaffected by acetic acid, finely granular, and generally without nucleoli. The cells are rounded or slightly polyhedric, pale, clear, or very slightly granular, and contain bodies similar to the free nuclei. The free nuclei are from $\frac{1}{5000}$ to $\frac{1}{4000}$ of an inch in diameter, and the cells measure from $\frac{1}{2500}$ to $\frac{1}{2000}$, and sometimes $\frac{1}{1400}$ of an inch.[3] These elements also exist in the second layer of the retina.

There has been a great deal of discussion with regard to the presence or absence of connective-tissue elements in the cerebro-spinal centres. In the other ganglia, there has never been any doubt with regard to the presence of connective tissue in greater or less amount, and in the cerebro-spinal centres there can hardly be any question of the existence of an exceedingly delicate stroma, chiefly in the form of stel-

[1] SCHULTZE, in STRICKER, *Manual of Human and Comparative Histology*, London, 1870, vol. i., p. 173, *et seq.*

[2] KÖLLIKER, *Éléments d'histologie humaine*, Paris, 1868, p. 329.

[3] LITTRÉ ET ROBIN, *Dictionnaire de médecine*, Paris, 1865, Article, *Myélocytes.*

late, branching cells, serving, in a measure, to support the nervous elements.

The blood-vessels of the nerve-centres form an exceedingly graceful capillary net-work with very large meshes. The gray substance is much richer in capillaries than the white.

A remarkable peculiarity of the vascular arrangement in the cerebro-spinal centres has already been described in connection with the lymphatic system. The blood-vessels here are surrounded by what have been called perivascular canals, first described by Robin, and afterward shown by His and Robin to be radicles of the lymphatic system.[1]

Composition of the Nervous Substance.

Our knowledge of the chemical constitution of the nervous system is, in many regards, quite unsatisfactory; but these tissues contain certain elements that have been very well determined. The chemical characters of cholesterine, for example, have long been known to physiologists, as well as the fact that this principle is a constant constituent of the nervous substance, united in some way with the other proximate principles, so that it does not appear in a crystalline form. Since we demonstrated, in 1862, the relations of cholesterine to the process of disassimilation, this principle has assumed its proper place as one of the most important of the products of physiological waste of the organism. The origin and function of cholesterine, with the processes for its extraction from the fluids and tissues of the body, have been fully considered under the head of excretion.[2]

Regarding cholesterine as an excrementitious product, to be classed with principles destined simply to be eliminated from the organism, the nerve-substance proper has been found to contain the following proximate principles, the chemical properties of which have been more or less

[1] See vol. ii., Absorption, p. 433. [2] See vol. iii., Excretion, p. 267, *et seq.*

accurately determined; viz., protagon, neurine, fatty matters combined with phosphorus, and bases combined with peculiar fatty acids.

Protagon.—This principle was discovered by Liebreich, and described in 1865.[1] Its formula is $C_{116}H_{241}O_{22}N_4P$. It may be extracted by the following process: The cerebral substance is bruised in a mortar, and afterward shaken with water and ether in a closed vessel. The mixture is then exposed to a temperature of 32° Fahr., and the ethereal layer, containing cholesterine, is removed. The insoluble mass is then extracted with alcohol, 85 per cent., at 113°, is again filtered and exposed to a temperature of 32°. An abundant precipitate then separates, which is washed with ether and desiccated *in vacuo*. The protagon is thus obtained in the form of a white powder. Since this principle has been described in the brain-substance, a compound analogous to, if not identical with protagon, has been discovered by Hermann in the blood-corpuscles.[2] In its general and chemical characters, protagon resembles the albuminoid proximate principles; but it presents the remarkable difference, that the sulphur, which exists in many of the principles of this class, is replaced by phosphorus.

Neurine.—This name has been applied to a rather indefinite principle supposed to represent the albuminoid element of the nervous tissue; but its characters as a proximate constituent of the nerve-substance have never been well determined. Robin and Verdeil place neurine among the proximate principles of probable existence. According to these authors, this is the organic substance of the brain, not soluble

[1] Liebreich, *Ueber die chemische Beschaffenheit der Gehirnsubstanz.—Annalen der Chemie und Pharmacie*, Leipzig und Heidelberg, 1865, Bd. cxxxiv., S. 29, *et seq.*

[2] Hermann, *Ueber das Vorkommen von Protagon im Blute.—Archiv für pathologische Anatomie und Physiologie*, Berlin, 1866, S. 36, *et seq.*

in alcohol. When incinerated it does not leave a residue impregnated with phosphoric acid, like the cerebral fatty matter.[1] According to more recent investigations, particularly those of Liebreich, neurine is a derivative of protagon. The neurine of Liebreich is obtained by boiling protagon for twenty-four hours in baryta-water, when there is formed the phospho-glycerate of baryta, and a new base, neurine.[2] It is evident that this substance cannot properly be regarded as a well-determined proximate principle.

We have already alluded to the experiments of Wurtz upon the synthesis of neurine.[3] These observations are important as a step toward the synthesis of organic nitrogenized principles, but they do not afford an example of the actual formation of a characteristic nitrogenized constituent of the nerve-tissue. They simply show that the chlorohydrate of an artificial organic compound presents crystals identical with the chlorohydrate of neurine extracted from the brain.[4]

Cerebral Fatty Principles.—Researches into the composition of the fatty principles found in the nervous substance have been so indefinite and unsatisfactory in their results, that even now they possess but little physiological interest. In the earlier observations, the fats extracted from the nerve-tissue were generally combined with cholesterine. This substance has now been isolated, and the residue contains a variety of principles, which seem, under physiological condi-

[1] Robin et Verdeil, *Traité de chimie anatomique*, Paris, 1853, tome iii., p. 451.

[2] Liebreich, *loc. cit.;* and, *Journal de l'anatomie*, Paris, 1866, tome iii., p. 654.

[3] See vol. iii., Excretion, p. 195, foot-note.

[4] Wurtz, *Sur l'identité de la nevrine artificielle avec la nevrine naturelle.—Comptes rendus*, Paris, 1868, tome lxvi., p. 772, *et seq.* Wurtz obtained neurine by the reaction of trymethylamine upon monochlorohydric glycol. He found that the chlorohydrate of trymethyloxethylammonium was identical with the chlorohydrate of neurine prepared with neurine from the brain. By neurine, Wurtz undoubtedly means the principle described under that name by Liebreich.

tions, to be intimately united with the nitrogenized substance, presenting one of the exceptions to the general law that fats exist in the body, uncombined, except with each other. In this mass of fatty matter, we can determine the presence of oleine, margarine, and stearine; but these are combined with other fats, fatty acids, etc., the remarkable peculiarity of most of which is, that they contain a certain proportion of phosphorus. These peculiar principles have received a variety of names, as they have been described more or less minutely by different observers, such as cerebrine, white and red phosphorized fat, lecithene, cerebric acid, and cerebrate of soda. The application of most of these names is very indefinite, and when we say that the substances are, in greatest part, peculiar to the nervous tissue, and that they contain phosphorus, we have stated about all that is physiologically important. Lecithene is a neutral phosphorized fat, probably composed of a number of different fatty principles, which exists, not only in the nervous substance, but in the blood, bile,[1] and the yolk of egg.[2] Its chemical history has no physiological interest. The same may be said of cerebric acid, the cerebrate of soda, oleo-phosphoric acid and its compounds with soda and lime.

Corpora Amylacea.—Little rounded or ovoid bodies, about $\frac{1}{1800}$ of an inch in diameter, have been described by Virchow and others[3] as existing normally in the corpora striata, the medulla oblongata, and some other portions of the cerebro-spinal system. With regard to the actual composition of these bodies, there is considerable difference of opinion. Virchow and many others regard them as identical with starch, the granules of which they certainly resemble very closely, being of the same shape, with borders well

[1] See vol. iii., Excretion, p. 262.

[2] Littré et Robin, *Dictionnaire de médecine*, Paris, 1865, Article, *Lécithene.*

[3] Virchow, *Cellular Pathology*, Philadelphia, 1863, p. 320.

—— Dalton, *Human Physiology*, Philadelphia, 1867, p. 66.

defined, frequently presenting concentric laminæ and a hilum. When carefully treated, first with a solution of iodine and then with a little sulphuric acid, they assume a blue color. Some observers consider them as analogous to cellulose, others have supposed that they are formed of cholesterine, and others regard them as nitrogenized bodies.[1] These points are of purely anatomical interest, and the physiological relations of these bodies are not known.

Regeneration of the Nervous Tissue.

We do not propose to discuss fully the question of the regeneration of nerves after section or even excision of a portion of their substance, though it is one of great pathological interest; but in this connection will refer to some experiments recently made, in which it appears that it is possible for certain of the most important of the nerve-centres to be regenerated and their function restored after extirpation.

With regard to the simple reunion of nerves after division or excision, it has long been known that this takes place in the human subject and in the inferior animals, with restoration of function.[2] The new tissue connecting the divided extremities of the nerve seems to pass through the regular stages of development observed in the nerve-tissue of the embryon, the gelatinous fibres, or the fibres of Remak, first appearing, and these being subsequently developed into true nerve-tubes. In this process there is not a cicatrix, as in the skin or muscular tissue, but a development of new elements possessing the anatomical and physiological characters of the original structure.

[1] VIRCHOW, *loc. cit.*

—— LITTRÉ ET ROBIN, *Dictionnaire de médecine*, Paris, 1865, Article, *Corpuscle.*

[2] LAVERAN, *Recherches expérimentales sur la régénération des nerfs*, *Thèse*, Strasbourg, 1867. This memoir contains an elaborate review of the earlier experiments upon the regeneration of nerves, with some original observations of much interest.

The fact of the speedy and complete reunion of divided nerves has been taken advantage of by physiologists in experiments upon nerves of different functions. Many years ago, Flourens divided two mixed nerves, the trunks of which were near each other, and crossed them, connecting the central end of the one with the peripheral end of the other, and *vice versa.* Reunion of the extremities thus attached took place, and the functions of the paralyzed parts were restored. The communication through both nerves was restored and corresponded to the artificial crossing of the nerves. In these experiments there was complete reunion of the extremities of different nerves possessing the same general properties. Flourens then attempted to produce, in the same way, an anatomical and physiological reunion between the divided extremities of nerves of different properties, as the pneumogastric and the fifth cervical. At the end of three months the anatomical reunion was found complete; but on dividing the other pneumogastric, to ascertain if the function of the first had been restored, the animal manifested the symptoms that follow division of both pneumogastrics, and died in two days.[1] These experiments have lately been repeated and extended by Gluge and Thiernesse,[2] Philipeaux and Vulpian,[3] and others, with more definite results. Gluge and Thiernesse, Schiff,[4] and Landry[5] failed to observe restoration

[1] FLOURENS, *Recherches expérimentales sur les propriétés et les fonctions du système nerveux*, Paris, 1842, p. 266, *et seq.*

[2] GLUGE ET THIERNESSE, *Sur la réunion des fibres nerveuses sensibles avec les fibres motrices.—Journal de la physiologie*, Paris, 1859, tome ii., p. 686, *et seq.*

[3] PHILIPEAUX ET VULPIAN, *Note sur des expériences démontrant que des nerfs séparés des centres nerveux peuvent, après s'être altérés complétement, se régénérer tout en demeurant isolés de ces centres, et recouvrer leurs propriétés physiologiques.—Journal de la physiologie*, Paris, 1860, tome iii., p. 214; *Recherches expérimentales sur la réunion bout à bout de nerfs de fonctions différents.*—Ibid., 1863, tome vi., p. 421, *et seq.*, and p. 474, *et seq.*

[4] SCHIFF, *Remarques sur les expériences de MM. Philipeaux et Vulpian sur la régénération des nerfs.—Journal de la physiologie*, Paris, 1860, tome iii., p. 217.

[5] LANDRY, *Réflexions sur les expériences de MM. Philipeaux et Vulpian, relatives à la régénération des nerfs.*—Ibid., p. 218.

of the function of nerves of different properties that became reunited after division. The experiments upon this point by Gluge and Thiernesse were the most extended, and were made upon the lingual branch of the fifth pair and the sublingual. In from three to six weeks, the central end of the sensitive nerve became firmly united with the peripheral end of the motor nerve, but the physiological union was in no case observed, except in one experiment in which the central end of the sublingual was involved in the reunion.[1] This conclusion was arrived at after a failure to obtain movements in the tongue by stimulating the lingual branch of the fifth above the point of union.

It is evident that these experiments must have an important bearing upon our theories concerning the mode of conduction of motor stimulus and sensitive impressions by the different nerves, and they will be referred to again in connection with that part of our subject. At present we can only refer to the positive results obtained by Philipeaux and Vulpian, which are in opposition to the negative experiments of the observers cited above. These physiologists succeeded in uniting, in dogs, the central end of the pneumogastric with the peripheral end of the sublingual, and the central end of the lingual branch of the fifth with the peripheral end of the sublingual, all of the nerves being divided, and, in the case of the sublingual and the lingual branch of the fifth, the central end of the motor nerve being torn out. In these experiments, on exposing the nerves four or five months after the first operation, irritation applied to the sublingual below the point of union produced pain, and a stimulus applied to the lingual branch of the fifth above the point of union excited movements of the tongue, even after dividing the nerve above and separating it from the centres, so that it was impossible for any reflex movements to take place.[2] These facts show that not only does union take

[1] Gluge et Thiernesse, *loc. cit.*, p. 695.

[2] See the memoirs by Philipeaux and Vulpian, already cited from the

place in nerves after division, and between the divided extremities of two different nerves having the same properties, but that the divided extremity of a motor nerve may be made to form an anatomical and physiological union with the divided extremity of a nerve of sensation, and that both motor and sensitive currents may be conducted through the fibres at the point of union.

The only remaining point of physiological interest connected with the regeneration of the nervous tissue is involved in the recent observations of Voit on the regeneration of the cerebral lobes after removal in a pigeon, and those of Masius and Vanlair upon the anatomical and functional regeneration of the spinal cord in frogs.

The experiments recorded by Voit, and his deductions, are very curious, and have given rise to a great deal of comment and criticism. In one observation, the cerebral lobes were removed from a young pigeon in the usual way, an operation very easily performed, and one which we practise yearly as a class-demonstration. It is particularly stated that the operation was complete, and that the entire posterior lobes were removed. Immediately after the operation, the pigeon presented the condition of stupor ordinarily observed. As he gradually recovered from this condition, he began to execute a number of mechanical movements, which it is unnecessary to detail fully, in the most extraordinary manner. The animal continued to improve, ceased the mechanical movements, and began to fly about, exhibiting timidity when approached, and, in short, seemed, after a time, to have quite or nearly returned to the normal condition. One thing, however, was remarked: the animal never took food (it was probably kept alive by stuffing, as is frequently done in such experiments). After five months, the pigeon was killed. The cranial cavity was found to be filled with a white mass, occupying the place from which the cerebrum had been re-

Journal de la physiologie; and, Vulpian, *Leçons sur la physiologie générale et comparée du système nerveux*, Paris, 1866, p. 280, *et seq.*

moved. This mass had the consistence of the white substance of the brain, and presented a perfect continuity with the cerebral peduncles, which had not been removed. It had the form of the two hemispheres, presenting a cavity filled with liquid and a septum. The whole mass consisted of perfect primitive fibres of double contour, and, in their meshes, ganglionic cells.[1]

This observation is certainly one of the most remarkable on record, and, from the extraordinary character of its results, would hardly be accepted for a moment, but for the established reputation of Prof. Voit. As it is, such an observation demands full confirmation. It is well known to all who have been in the habit of removing the cerebral lobes, that it is absolutely necessary to remove every portion of their substance, in order to obtain uniform results, and that this is accomplished sometimes with considerable difficulty. In demonstrations to a medical class, we have frequently verified this fact, and have observed recovery, more or less complete, when but a small portion of the posterior lobes escaped. This criticism upon the remarkable observation just detailed is made by Vulpian,[2] and its pertinence will be recognized by every practical physiologist. We have only to study the experiments first made by Flourens, to learn how, in the lower animals, a part of one of the great central ganglia may gradually assume the function of the whole, after this function has been interrupted by the first mutilation.[3]

We have cited the essential points in this observation because it has been so extensively commented upon by physiologists, but it is far from establishing the principle that a great nervous centre, like the cerebrum, may be anatomically and functionally regenerated after extirpation.

[1] C. Voit, *Phénomènes qui suivent l'ablation des hémisphères du cerveau chez les pigeons* (*Académie des Sciences de Munich*), *traduit de l'allemand par le Dr.* Rabuteau.—*Revue des cours scientifiques*, Paris, 1869, tome vi., p. 256.

[2] Vulpian, *Archives de physiologie*, Paris, 1869, tome ii., p. 302.

[3] Flourens, *Recherches expérimentales sur les propriétés et les fonctions du système nerveux*, Paris, 1842, p. 100.

The general results of the experiments of Masius and Vanlair upon the regeneration of parts of the spinal cord in frogs, after loss of a small portion of its substance, show that such reparation may take place and is attended with restoration of function. The formation of cells precedes the development of fibres, and voluntary motion appears in the parts situated below the lesion, before sensation.[1] There are no instances on record of such regeneration in the human subject or in the warm-blooded animals.

[1] Masius et Vanlair, *Recherches expérimentales sur la régénération anatomique et fonctionnelle de la moelle épinère*, Bruxelles, 1870.

CHAPTER II.

MOTOR AND SENSORY NERVES.

Distinct seat of the motor and sensory properties of the spinal nerves—Speculations of Alexander Walker—Views of Sir Charles Bell regarding the functions of the anterior and posterior roots of the spinal nerves—Experiments of Magendie on the roots of the spinal nerves—Properties of the posterior roots of the spinal nerves—Influence of the ganglia upon the nutrition of the posterior roots—Properties of the anterior roots of the spinal nerves—Recurrent sensibility—Mode of action of the motor nerves—Associated movements—Mode of action of the sensory nerves—Sensation in amputated members.

The physiological property of nerves which enables them to conduct to and from the centres the impressions, stimulus, force, or whatever the imponderable nervous agent may be, is one inherent in the tissue itself, belonging to no other structure, and is dependent for its continuance upon proper conditions of nutrition. So long as the nerves maintain these conditions, they retain this characteristic physiological property, which is generally known under the name of irritability.

Aside from the special senses, the sense of temperature, and of weight, it is known to every one that through the nerves we appreciate what are called ordinary sensations, and are enabled to execute voluntary movements. If a nerve distributed to a part endowed with sensation and the power of motion be divided, both of these properties are lost, and can only be regained through a reunion of the divided nerve. Again, it is equally well known that if such a nerve be exposed in its course and irritated, violent movements take place in the muscles to which it is distributed, and pain is appreciated, referred to parts supplied from the

same source. These facts, which were fully appreciated by the ancients, show that the general system of nerves is endowed with motor and sensory properties, the question being simply whether these be inherent in the same fibres or belong to fibres physiologically distinct and derived from different parts of the central system. This question, which was solved only about half a century ago, will be the first to engage our attention.

Distinct Seat of the Motor and Sensory Properties of the Spinal Nerves.—All of the nerves that take their origin from the spinal cord are endowed with motor and sensory properties. These nerves supply the whole body, except the head and other parts receiving branches from the cranial nerves. They arise by thirty-one pairs from the sides of the spinal cord, and each nerve has an anterior and a posterior root. The anatomical differences between the two roots are that the anterior is the smaller, and has no ganglion. The larger, posterior root presents a ganglionic enlargement in the intervertebral foramen. Just beyond the ganglion, the two roots coalesce and form a single trunk. The nerve-fibres in the two roots are not of the same size, the anterior fibres measuring on an average about one-fourth more than the posterior fibres.[1] The structure of the ganglia of the posterior roots has already been considered sufficiently in detail.[2]

It would be unprofitable to discuss the vague ideas of the older anatomists and physiologists with regard to the properties of the roots of the spinal nerves, and we can date our information upon this point from the suggestion of Alexander Walker, in 1809, that one of these roots was for sensation alone and the other for motion.[3] It is most remarkable, however, that Walker, from purely theoretical considera-

[1] KÖLLIKER, *Éléments d'histologie humaine*, Paris, 1868, p. 339.

[2] See page 51.

[3] WALKER, *New Anatomy and Physiology of the Brain in particular and of the Nervous System in general.—Archives of Universal Science*, Edinburgh, 1809, vol. iii., pp. 173, 174.

tions, should have stated that the posterior roots were motor and the anterior roots sensory, precisely the reverse of the truth, and should have advanced this view in a publication as late as 1844.[1] In the work alluded to, which contains some of the most extraordinary pseudo-scientific vagaries ever published, it is curious to see how near Walker came to the greatest discovery in physiology since the description of the circulation of the blood. He gives an account of an experiment as follows: "On opening the spinal canal of a frog, accordingly, and performing the only operation on a living animal which he ever has performed, or ever will perform, he found that, in perfect conformity with previous reasoning, irritation of the anterior roots caused motion, and irritation of the posterior roots caused little or none."[2] Now, it does not appear in the work from which this quotation is made at what time this experiment was performed; and we have not been able to ascertain that it was done before 1811; but, correctly interpreted, this observation had been almost the great discovery. To conclude our review of the claims of Walker, there can be no doubt of the fact that he was the first to distinctly assign motion and sensation to the different roots of the spinal nerves, though he incorrectly ascribed motor properties to the posterior roots and sensory properties to the anterior, and brought forward not one iota of proof in support of his theories.

The claims of Mayo to the discovery of the distinct properties of the roots of the spinal nerves are very indefinite. He simply states, long after the publication of the experiments of Magendie, that the "remarkable analogy which exists between the fifth nerve and the spinal nerves

[1] WALKER, *The Nervous System, anatomical and physiological: in which the functions of the various parts of the brain are for the first time assigned, and to which is prefixed some account of the author's earliest discoveries, of which the more recent doctrine of Bell, Magendie, etc., is shown to be at once a plagiarism, an inversion, and a blunder, associated with useless experiments, which they have neither understood nor explained*, London, 1844, p. 50, *et seq.*

[2] WALKER, *op. cit.*, p. 18.

led me to suppose that the two roots of the spinal nerves had the same discrepancy of function with the two roots of the fifth; and that the ganglionic portion might belong to sensation, the smaller anterior portion to volition."[1]

As we shall see farther on, all discussion relative to priority in the discovery of the true functions of the roots of the nerves is confined to the claims of Bell and of Magendie. The experiments of Müller[2] and others were made after 1822, the date of the first publication of the experiments of Magendie.

In nearly every treatise on physiology published since 1822, and in almost all works on the nervous system subsequent to that date, the great discovery of the distinct seat of motion and sensation in the spinal nerves is ascribed to Sir Charles Bell. The name of Magendie is seldom mentioned in this connection, even in France; and his discoveries are supposed to relate chiefly to the seat of sensation and motion in the different columns of the spinal cord.

It is unnecessary to enlarge upon the importance of the discovery that the anterior roots of the spinal nerves are motor, and the posterior, sensory, and that the union of these two roots in the mixed nerves gives them their double properties, for we can hardly imagine a physiology of the cerebro-spinal nervous system without this fact as the starting-point; and we have entered, rather more elaborately than usual, into an historical review of this discovery, from the fact that nearly all writers have ascribed it to Sir Charles Bell, and have ignored the claims of Magendie, the real discoverer. In an article published in English, in October, 1868,[3] and in French, during the same year,[4] we have given

[1] MAYO, *Outlines of Human Physiology*, London, 1827, p. 240.

[2] MÜLLER, *Physiologie du système nerveux*, Paris, 1840, tome i., p. 85, *et seq.*; and, *Manuel de physiologie*, Paris, 1851, tome i., p. 598, *et seq.* The experiments of Müller were first published in 1831.

[3] FLINT, JR., *Historical Considerations concerning the Properties of the Roots of the Spinal Nerves.—Quarterly Journal of Psychological Medicine*, New York, 1868, vol. ii., p. 625, *et seq.*

[4] *Journal de l'anatomie*, Paris, 1868, tome v., p. 520, *et seq.*, and p. 575, *et seq.*

an elaborate review of the whole subject, being prompted to do so by the perusal of what purported to be an exact reprint of the original pamphlet by Charles Bell.[1] This pamphlet was printed for private circulation in 1811, and was never published. It has been entirely inaccessible, and its contents were only to be divined by references and quotations in the subsequent writings of Sir Charles Bell and of his brother-in-law, Mr. Shaw.

Physiological literature does not present another instance of the merit of a great discovery resting upon references to an unpublished pamphlet, which no student could possibly consult in the original, none of these references, upon close analysis, proving to be entirely distinct and satisfactory. It is not to be wondered at, therefore, that in our study of the origin of one of the greatest discoveries of all ages, a reprint of the original memoir should be examined with the most critical care. That this reprint was correct, seemed probable from a comparison of its text with the quotations from the original to be found in the writings of Sir Charles Bell and Mr. Shaw, and from the testimony of reviewers who claimed to have compared it with the original.[2] Within a short time, however, an authorized reprint in full, from a manuscript in the hands of the widow of the author, has appeared in the *Journal of Anatomy*.[3] This reprint corresponds exactly with the text in the "*Documents and Dates*."

When the only reprint of the celebrated pamphlet of Sir Charles Bell was itself excessively rare, as is the case with the "*Documents and Dates*," we thought it desirable to make long quotations to show the ideas entertained by

[1] *Documents and Dates of Modern Discoveries in the Nervous System*, London, John Churchill, 1839, p. 37, *et seq.*

[2] *The London Medical and Physical Journal*, 1829, vol. lxii., p. 525, and vol. lxiii., p. 40. *The British and Foreign Medico-Chirurgical Review*, London, 1840, vol. ix., p. 98.

[3] *Reprint of the "Idea of a new Anatomy of the Brain; submitted for the Observations of his Friends*," by CHARLES BELL, F. R. S. E.—*Journal of Anatomy and Physiology*, Cambridge and London, 1869, vol. iii., p. 147, *et seq.*

Bell regarding the properties of the two roots of the spinal nerves; but now that an authorized reprint can be so readily consulted, it is only necessary to refer to this to show that Bell did not at that time regard the anterior roots as motor and the posterior roots as sensory, but that he thought that the anterior roots were for both motion and sensation and the posterior roots presided over "the secret operations of the bodily frame, or the connections which unite the parts of the body into a system."[1]

All the credit which we have to give to Sir Charles Bell for advances in the anatomy and physiology of the spinal nerves must cease with the review of the pamphlet of 1811. In a memoir on the nerves of the head, read before the Royal Society, July 12, 1821, more than a year before the publication of the experiments of Magendie, there is no mention of distinct motor and sensitive roots of the spinal nerves, nor of distinct properties in different portions of the spinal cord. This paper was republished by Bell, after the publication of Magendie's observations, in a work on the nervous system; and it is this republication which is most accessible and most frequently referred to by physiological writers. The republication avowedly contains "some additional explanations;" but a careful comparison of it with the original shows that every portion of it that was susceptible of such verbal alteration had been modified to make it correspond with the discovery by Magendie. But, at the same time, the impression received by the reader is, that it is essentially the same as the memoir published in 1821.[2] In the controversial condition of the question at the time of this republication, the alterations and "additional explanations" ought certainly

[1] In a paper read before the Medico-Chirurgical Society, in April, 1822, Mr. J. Shaw gives the date of the first paper by Charles Bell, as 1809. This error is quoted into many reviews and other publications, but it has been corrected by Bell himself, and by Mr. A. Shaw. (ALEXANDER SHAW, *Narrative of the Discoveries of Sir Charles Bell in the Nervous System*, London, 1830, p. 14.)

[2] CHARLES BELL, *The Nervous System of the Human Body*, London, 1844, p. 33 *et seq.*

to have been distinctly indicated in the text; but in a reprint of the paper of 1821, in 1830, there is no indication to the reader that any change had been made from the original, though every expression bearing upon the question is made to correspond with the information derived from the discoveries of Magendie.[1] This is a subject which we have no desire to pursue farther than is necessary to vindicate the

[1] Charles Bell, *The Nervous System of the Human Body, embracing the Papers delivered to the Royal Society on the Subject of the Nerves*, London, 1830, p. 55, *et seq.*

In the appendix to the work on the Nervous System, published in 1844, the claim to the discovery of the distinct functions of the anterior and posterior roots of the spinal nerves is distinctly made by Sir Charles Bell, who refers to the experiments detailed in the pamphlet of 1811. It will be seen by the following extract, as compared with the extracts which we have made from the pamphlet, that the statements by Sir Charles Bell as to what was contained in this pamphlet are incorrect and calculated to convey an erroneous idea with regard to the nature of the observations, printed in 1811, but inaccessible, and of the deductions made at that time.

"Long before this (1811) I wrote a little book, put it into the hands of my friends, and had it printed and distributed; it contained (excuse me in saying it) this great principle—that a nerve, whatever its nature may be, cannot perform two functions at once; it cannot convey sensation inward to the sensorium at the same moment that it carries outward a mandate of the will to the muscles, whether it be through the means of a fluid, or an ether, or a vibration, or what you will, that it performs its function. Two vibrations cannot run counter through the same fibre, and at the same instant; two undulations cannot go in different directions through the same tube at the same moment; and therefore I conceived that the nerves must be different in their kind. This led me to experiment upon the nerves of the spine; for I said: 'Where shall I be able to find a nerve with the roots separated? Where shall I be able to distinguish the properties of a compound nerve? By experimenting upon the separate roots of the spinal nerves.' So, then, taking a fine instrument, the point of a needle, and drawing it first along one set of roots, and then along the other, I found that, as I touched one set—the anterior roots—it was like touching the key of a piano-forte, all the cords, as it were—the muscles—were in vibration; and when I touched the other there was pain and struggling. That would not do; the animal being alive to sensation, there was confusion here; and therefore I struck the animal on the head, and then I made my experiments clearly; by which it was shewn, that the roots of these nerves were of different qualities, one obviously bestowing *motion;* and, by inference, the other bestowing *sensibility*" (*The Nervous System*, etc., London, 1844, p. 285).

scientific record of the last-named physiologist; and if the good taste of these allusions be called in question, we have only to ask that the review in the *Psychological Journal* or in the *Journal de l'anatomie* be consulted, and that the comparisons there made be verified. The same criticisms of the alterations in the republished memoirs of Sir Charles Bell have been made by Vulpian.[1] Among English writers, the relative claims of Bell and Magendie have been correctly reviewed by a writer in the *London Medical and Physical Journal*, in 1829,[2] and by Elliotson, in 1840.[3] Bernard, who formerly ascribed the discovery to Bell, has lately recognized fully the claims of Magendie.[4]

The first publications of Magendie concerning the anatomy and the functions of different portions of the nervous system appeared in the *Journal de physiologie*, in 1821. In the first volume of this journal, is a notice of the researches of Charles Bell on the nerves of the face, with an account of the observations of Mr. Shaw on the same subject.[5] Magendie here states that he repeated the experiments of Bell with MM. Shaw and Dupuy at Alfort.[6] He had not at that time received the memoir of Bell; but in a succeeding num-

[1] VULPIAN, *Leçons sur la physiologie générale et comparée du système nerveux*, Paris, 1866, pp. 109 and 127.

[2] *The London Medical and Physical Journal*, 1829, vol. lxii., p. 532.

[3] ELLIOTSON, *Human Physiology*, London, 1840, p. 465.

[4] BERNARD, *Leçons sur la physiologie et la pathologie du système nerveux*, Paris, 1858, tome i., p. 20, *et seq.* Even Bernard, a pupil, and for a long time the *préparateur* for Magendie, at one time seemed to regard Sir Charles Bell as the discoverer of the functions of the roots of the spinal nerves (ibid., p. 25; and, *Leçons sur les effets des substances toxiques et médicamenteuses*, Paris, 1857, p. 20); in a late work, however, in which this whole subject is reviewed, the claims of Magendie to the discovery are fully recognized (BERNARD, *Rapport sur le progrès et la marche de la physiologie générale en France*, Paris, 1867, pp. 12 and 154). Bernard states that he was unable to obtain the original memoir of Bell, printed in 1811, but finally procured an exact copy, which is probably the reprint of 1839. (Ibid., p. 155.)

[5] CHARLES BELL, *Recherches anatomiques et physiologiques sur le système nerveux.—Journal de physiologie*, Paris, 1821, tome i., p. 384, *et seq.*

[6] *Loc. cit.*, p. 387.

ber of the journal, he gives a full analysis of it.[1] In this number, also, he speaks of having repeated the experiments. In the same journal, follows a translation of the experiments of Mr. Shaw.[2] In none of these publications is there any allusion to the properties of the anterior and posterior roots of the spinal nerves, nor is there any evidence that either Bell, Shaw, or Magendie knew any thing about the distinct seat of motion and sensation in the spinal cord and the spinal nerves.[3]

In August, 1822, Magendie published his first experiments on the functions of the roots of the nerves.[4] Unlike any of the observations made by Charles Bell on the spinal nerves, these were made upon living animals. The spinal canal was opened, and the cord, with the roots of the nerves, exposed. The posterior roots of the lumbar and sacral nerves were then divided upon one side and the wound united with sutures. The result of this observation was as follows:

"I thought at first that the limb corresponding to the divided nerves was entirely paralyzed; it was insensible to pricking and to the most severe pinching, it also appeared to me to be motionless; but soon, to my great surprise, I saw it move in a very marked manner, although the sensibility was still entirely extinct. A second, a third experiment, gave me exactly the same result; I commenced to regard it as probable that the posterior roots of the spinal nerves might have functions different from the anterior roots, and that they were more particularly devoted to sensibility."[5]

[1] Bell, *Suite de recherches anatomiques et physiologiques sur le système nerveux.—Journal de physiologie*, Paris, 1822, tome ii., p. 66, *et seq.*

[2] Shaw, *Expériences sur le système nerveux. Extrait et traduit de l'Anglais par M. Cairns.—Journal de physiologie*, Paris, 1822, tome ii., p. 77, *et seq.*

[3] In the same volume of the journal (p. 363), Magendie gives an account of Bell's observations on the respiratory nerves of the chest, which were presented to the Royal Society, May 2, 1822.

[4] Magendie, *Expériences sur les fonctions des racines des nerfs rachidiens.—Journal de physiologie*, Paris, 1822, tome ii., p. 276, *et seq.*

[5] Ibid., p. 277.

The experiments in which the anterior roots were divided were no less striking:

"As in the preceding experiments, I only made the division upon one side, in order to have a term of comparison. One can conceive with what curiosity I followed the effects of this division; they were not at all doubtful, the limb was completely motionless and flaccid, while it preserved a marked sensibility. Finally, that nothing should be neglected, I divided at the same time the anterior and the posterior roots; then followed absolute loss of sensation and of motion." [1]

From these experiments Magendie drew the following conclusions:

"I am following out my researches, and will give a more detailed account of them in the following number; it is sufficient for me to be able to announce at present as positive, that the anterior and the posterior roots of the nerves which arise from the spinal cord have different functions, that the posterior seem more particularly devoted to sensibility, while the anterior seem more especially connected with motion." [2]

In the second note, published in the same volume of the *Journal de physiologie*, Magendie exposed and irritated the two roots of the nerves, with the following results:

"I commenced by examining in this regard the posterior roots, or the nerves of sensation. The following is the result which I observed: on pinching, pulling, or pricking these roots, the animal manifested pain; but this was not to be compared as regards intensity with that which was developed if the spinal cord were touched, even lightly, at the point of origin of the roots. Nearly every time that the posterior roots were thus stimulated, contractions were produced in the muscles to which the nerves were distributed; these contractions, however, are not well marked, and are infinitely more feeble than when the cord itself is

[1] Ibid., p. 278. [2] Ibid., p. 279.

touched. When, at the same time, a bundle of the posterior root is cut, there is produced a movement in totality in the limb to which the bundle is distributed.

"I repeated the same experiments on the anterior roots, and I obtained analogous results, but in an opposite sense; for the contractions excited by the contusion, the pricking, etc., are very forcible, and even convulsive, while the signs of sensibility are hardly visible. These facts are, then, confirmatory of those which I have announced; only they seem to establish that sensation is not exclusively in the posterior roots, any more than motion in the anterior roots. Nevertheless, a difficulty may arise. When, in the preceding experiments, the roots had been cut, they were attached to the spinal cord. Might not the disturbance communicated to the cord be the real cause either of the contractions or of the pain which the animals experienced? To remove this doubt, I repeated the experiments after having separated the roots from the cord; and I must say that, except in two animals, in which I saw contractions when I pinched or pulled the anterior and posterior roots, in all the other instances I did not observe any sensible effect of irritation of the anterior or posterior roots thus separated from the cord."[1]

Magendie then goes on to say that, when he published the note in the preceding number of the journal, he supposed that he was the first who had thought of cutting the roots of the spinal nerves; but he was soon undeceived by a letter from Mr. Shaw, who stated that Bell had divided the roots thirteen years before. Magendie afterward received from Mr. Shaw a copy of Bell's essay ("Idea of a New Anatomy of the Brain"), and, as will be seen by the following extract, gave Bell full credit for all his observations:

"It is seen by this quotation from a work which I could not be acquainted with, inasmuch as it had not been published, that Mr. Bell, led by his ingenious ideas concerning

[1] Ibid., p. 368.

the nervous system, was very near discovering the functions of the spinal roots; still the fact that the anterior are devoted to movement, while the posterior belong more particularly to sensation, seems to have escaped him; it is, then, to having established this fact in a positive manner that I must limit my pretensions."[1]

Such are the experiments by which the properties of the roots of the spinal nerves were discovered. From that time, the fact took its place in science, that the posterior roots are for sensation and the anterior for motion. Some discussion has arisen as to whether the anterior roots do not possess a certain amount of sensibility, called recurrent sensibility, and this question has engaged the attention of physiologists within a few years; but the distinct functions of the two roots have never been doubted. We have already seen what use Bell made of these facts in late editions of his work on the nervous system. Before the days of anæsthetics, exposing the roots of the nerves in the dog was very laborious, and painful to the animal, and the disturbances produced by so serious an operation interfered somewhat with the effects of irritation of the different roots. But now that the canal may be opened without pain to the animal, the experiments are much more satisfactory and have often been repeated by physiologists. We have frequently, indeed, demonstrated the properties of the roots of the nerves in public teaching.[2]

Although, as we have seen, almost all physiological writers, even in France, regarded Bell as the real discoverer, Magendie continued to claim that he first positively ascertained the seat of motion and sensation in the spinal nerves.

[1] Ibid., p. 371.

[2] FLINT, JR., *Experiments on the Recurrent Sensibility of the Anterior Roots of the Spinal Nerves.—New Orleans Medical Times*, 1861, p. 21, *et seq.*

At the time that this paper was written, we had not had an opportunity of consulting the original memoir of Sir Charles Bell, and, with others, regarded him as the discoverer of the functions of the roots of the nerves. We have also had occasion to modify the views therein expressed concerning the recurrent sensibility of the anterior roots.

In 1823, after reiterating his statements with regard to the nerves, he extended his researches to the cord itself, and demonstrated that the anterior columns were motor and the posterior columns sensitive.[1] In all his subsequent publications the same statements are made.[2]

Shaw, in his "Narrative," states that, in 1822, Magendie "admitted that the experiments on the roots of the spinal nerves, which he had claimed as original, had been performed many years before by Sir Charles Bell."[3] This is not correct; and we have already quoted in full the passage in which Magendie gives Bell full credit for what he had done, but expressly states that the fact, that the anterior roots preside over movement, and the posterior, over sensation, seems to have escaped him. Shaw also quotes Desmoulins and Magendie as admitting "that there is no absolute distinction between the functions possessed by the two roots;"[4] but, in doing this, he translates the expression into English incorrectly. In the passage referred to, it is stated that "L'isolement des deux propriétés dans chacun des deux ordres de racines, n'est donc pas absolu," which simply means that the motor roots are not absolutely without sensibility, and the sensory roots are not absolutely devoid of motor properties.

The experiments of Magendie, made in 1822, must stand without further question as the first to demonstrate the true properties of the two roots of the spinal nerves; and, before the publication of these experiments, no physiologist had a correct idea, theoretical or experimental, of the seat of motion and sensation in these nerves.

[1] MAGENDIE, *Note sur le siége du mouvement et du sentiment dans le moelle épinère.—Journal de physiologie*, Paris, 1823, tome iii., p. 153, *et seq.*

[2] DESMOULINS ET MAGENDIE, *Anatomie des systèmes nerveux des animaux à vertèbres*, Paris, 1825, tome ii., p. 777.

MAGENDIE, *Précis élémentaire de physiologie*, deuxième édition, Paris, 1825, tome i., pp. 167, 216; et, quatrième édition, 1836, tome i., pp. 200, 266.

[3] ALEXANDER SHAW, *Narrative of the Discoveries of Sir Charles Bell in the Nervous System*, London, 1839, p. 156.

[4] *Loc. cit.*, p. 168.

Properties of the Posterior Roots of the Spinal Nerves.—It is unnecessary to follow out, from the date of the first experiments by Magendie to the present day, the observations that have been made from time to time upon the properties of the roots of the spinal nerves. For many years, the difficulties in operating upon animals high in the scale rendered confirmatory experiments somewhat unsatisfactory. The great German physiologist, J. Müller, showed, in experiments made upon frogs, in 1831,[1] that irritation of the posterior roots produced no convulsive movements; but he despaired of operating satisfactorily upon warm-blooded animals. Magendie, in his later experiments,[2] and Longet, in experiments performed on dogs, published in 1841,[3] showed very satisfactorily that the posterior roots were exclusively sensory, and this fact has been abundantly confirmed by more recent observations upon the higher classes of animals. We have ourselves frequently exposed and irritated the roots of the nerves in dogs in public demonstrations, in experiments upon the recurrent sensibility of the anterior roots,[4] and in another series of observations upon the properties of the spinal cord, which will be referred to hereafter.

The remarkable anatomical peculiarity of the posterior roots, which they have in common with all of the exclusively sensitive nerves, is the presence of a ganglion. While we have no distinct idea of the function of these ganglia in connection with the transmission of impressions from the periphery to the centres, it has been shown to have a remark-

[1] Müller, *Nouvelles expériences sur l'effet que produit l'irritation méchanique et galvanique sur les racines des nerfs spinaux.—Annales des sciences naturelles*, Paris, 1831, tome xxiii., p. 100, *et seq.*

[2] Magendie, *Leçons sur les fonctions et les maladies du système nerveux*, Paris, 1841, tome ii., p. 52, *et seq.*, *quatrième leçon*, 3 mai, 1839.

[3] Longet, *Recherches pathologiques et expérimentales sur les propriétés et les fonctions des faisceaux de la moelle épinère et des racines des nerfs rachidiens.—Archives générales de médecine*, Paris, 1841, tome lvi., p. 168, *et seq.*

[4] Flint, Jr., *Experiments on the Recurrent Sensibility of the Anterior Roots of the Spinal Nerves.—New Orleans Medical Times*, 1861, p. 21, *et seq.*

able influence upon the nutrition of the nerves after their division. Operating upon the second cervical nerves, in which the ganglia can be reached without exposing the spinal cord, Waller has demonstrated the following interesting facts :[1]

When the roots are divided between the ganglion and the cord, the central end of the anterior root, attached to the cord, preserves its normal structure, while the peripheral end in a few days becomes degenerated, the tubes filled with granular matter, etc., and, in short, undergoes those changes observed in all nerves separated from their centres. On the other hand, in the posterior roots, the end attached to the cord undergoes degeneration, and the peripheral end, the one to which the ganglion is attached, preserves its normal histological characters. From these experiments, which have been confirmed and somewhat extended by Bernard,[2] it is concluded that the ganglia of the posterior roots have an influence over the nutrition of the sensitive nerves, in the same way as the centres influence the nutrition of the motor nerves which emanate from them. These points are interesting, as showing the existence of centres attached to the sensory system of nerves, which have, as far as we know, a purely trophic influence over the nerves, while the active centres to which the motor nerves are attached regulate, to a certain extent, the nutrition of the nerves, and also are capable of generating nerve-force. We do not know that the ganglia of the roots of sensitive nerves have any function except as trophic centres.

Properties of the Anterior Roots of the Spinal Nerves.—The same experiments that demonstrated that the posterior roots of the spinal nerves are sensitive showed that the anterior roots are motor. If the two roots be exposed in an

[1] WALLER, *Comptes rendus*, Paris, 1857, tome xliv., p. 168.

[2] BERNARD, *Leçons sur la physiologie et la pathologie du système nerveux*, Paris, 1858, tome i., p. 235, *et seq.*

animal just killed, no convulsive movements are produced by stimulating the posterior roots; but if the anterior roots be irritated, movements of the most violent character occur, confined to those muscles to which the filaments of the roots are distributed. There has never been any doubt upon this point since the experiments of Magendie; and it is now universally admitted by physiologists, that the motor properties of the mixed nerves are derived exclusively from their anterior roots of origin from the spinal cord. The question has arisen, however, whether the anterior roots be not also endowed with sensibility, notably less in degree than the posterior roots, but still marked and invariable. The sensibility observed in the anterior roots is abolished by section of the posterior roots; and this property, which is thought to be derived from the posterior roots, has been called recurrent sensibility.

Recurrent Sensibility.—We have seen, in reviewing the history of the discovery of the distinct function of the roots of the spinal nerves, that even in the earliest experiments by Magendie, it appeared that the anterior roots possessed sensibility in a certain degree, though it was insignificant as compared with the sensibility of the posterior roots. In his later experiments, Magendie formularized these facts, and announced that the anterior roots were sensitive as well as motor, but less sensitive than the posterior roots, and that this sensibility was abolished when the posterior roots were divided.[1] Later still, he failed to demonstrate this sensibility of the anterior roots; but it was finally shown that this occurred in animals exhausted from pain and loss of blood, and that the anterior roots were really sensitive under normal conditions.[2] Longet claims to have discovered, in 1839, what

[1] MAGENDIE, *Leçons sur les fonctions et les maladies du système nerveux*, Paris, 1841, tome ii., pp. 63, 78, *quatrième leçon*, 3 mai, 1839, *cinquième leçon*, 8 mai, 1839.

[2] MAGENDIE, *Note sur la sensibilité récurrente; Extrait des comptes rendus*, Paris, juin, 1847, tome xxiv., p. 3.

is now known as the recurrent sensibility of the anterior roots, and to have communicated his views to Magendie;[1] but the publications on the subject and the testimony of Bernard,[2] who witnessed all the experiments in the laboratory of the College of France, as well as the observations of Magendie, in 1822, leave no doubt that he was the first to note the sensibility of these roots.

The experimental facts with regard to the recurrent sensibility are very simple. If the two roots of a spinal nerve be exposed, and if the animal be allowed to recover, by a few hours' repose, from the shock of the operation, irritation of the posterior root will produce pain and the general movements incident to it, but no localized contractions of muscles; and irritation of the anterior root will produce contraction of certain muscles and a certain amount of pain, always less, however, than the pain resulting from stimulation of the posterior roots. If the anterior root be divided, the end attached to the cord will be found completely insensible, but the peripheral end will manifest the same sensibility as the undivided root; showing that the sensory properties of the anterior roots are not derived from the cord. If the posterior root be divided, the sensibility of the anterior root is instantly abolished; showing that the sensibility of the anterior root is recurrent, being derived from the posterior root through the periphery. With regard to these facts there can be no doubt, and we ourselves verified them in a series of experiments published in 1861.[3] Experiments have simply demonstrated the fact that the recurrent sensibility comes through the periphery, without actually showing any recurrent fibres; and division of a mixed nerve after the union of the two roots deprives the anterior root of its sen-

[1] Longet, *Traité de physiologie*, Paris, 1869, tome iii., p. 115.

[2] Bernard, *Leçons sur la physiologie et la pathologie du système nerveux*, Paris, 1858, tome i., p. 35.

[3] Flint, Jr., *Experiments on the Recurrent Sensibility of the Anterior Roots of the Spinal Nerves.—New Orleans Medical Times*, 1861, p. 21, *et seq.*

sibility, showing that the recurrent fibres, if they exist, must turn back near the periphery.[1]

The question now arises with regard to the exact mechanism of recurrent sensibility. The explanation offered by Magendie and Bernard is, that there are actually fibres returning from the posterior to the anterior roots; that these fibres are, of course, sensitive, and that irritation of the anterior roots is propagated toward the periphery, and returns to the centres through the posterior roots. This explanation satisfies all of the experimental conditions, and is further sustained by the microscopical examinations of Schiff, and of Philipeaux and Vulpian. It will be remembered that the ganglia of the posterior nerves, after division of these roots, have the remarkable power of preserving the anatomical integrity of the fibres to which they are attached. Now, it has been shown by Schiff that, after division of the posterior roots beyond the ganglia, the anterior roots contain altered fibres, which he believes come from the posterior roots, and give to these roots their sensibility. Philipeaux and Vulpian, in experiments on the regeneration of nerves, showed that the peripheral ends of the sublingual and facial nerves remained sensitive after division, and that after ten or fifteen days, in the midst of a great mass of degenerated fibres, were a few that possessed their normal characters.[2] The bearing of these facts will be better understood by referring back to the experiments of Waller on the influence of the ganglia over the nutrition of sensitive nerves.[3]

Dr. Brown-Séquard offers a different explanation of the pain developed upon irritation of the anterior roots. He believes this to be due entirely to cramp or convulsive contraction of the muscles.[4] This may be accepted, perhaps, as

[1] BERNARD, *Système nerveux*, Paris, 1858, tome i., p. 28.

[2] VULPIAN, *Leçons sur la physiologie générale et comparée du système nerveux*, Paris, 1866, p. 150.

[3] See page 80.

[4] BROWN-SÉQUARD, *Course of Lectures on the Physiology and Pathology of the Central Nervous System*, Philadelphia, 1860, p. 8.

a partial explanation; for there can be no doubt of the fact that violent muscular action, produced independently of volition, is more or less painful; but it does not explain the great sensibility sometimes observed when the muscular contraction is comparatively feeble. There can be hardly any doubt that the explanation offered by Magendie, and sustained by the ingenious histological observations cited above, is in the main correct.

Mode of Action of the Motor Nerves.—Having established the anatomical distinction between the motor and sensory nerves, it becomes necessary to study the differences in the mode of action of these two kinds of nervous conductors. In the first place, it is evident, taking the nerves and their roots as we find them in the organism in a normal condition, that certain fibres act from the centres to the periphery, conducting motor stimulus, while others act from the periphery to the centres, conducting sensory impressions; but within a few years, certain experiments have raised the question, whether sensory fibres may not be made to conduct the motor stimulus, and *vice versa*. The experiments to which we allude have already been referred to in connection with the regeneration of nerves;[1] and they show that when a sensory and a motor branch, situated near enough together, be divided, and the peripheral extremity of one be connected with the central extremity of the other, after a time union will take place, and the motor filaments will conduct sensory impressions, and the sensory filaments will conduct the motor stimulus. This is a most curious and interesting experimental fact; but it is no argument against the distinct seat of motion and sensation in the nervous system.

As regards the motor nerves, the force, whatever it may be, generated in the centres, is conducted from the centres to the peripheral distribution of the nerves in the muscles,

[1] See page 62.

and is here manifested by contraction. Their mode of action, therefore, is centrifugal. When these motor filaments are divided, the connection between the parts animated by them and the centre is interrupted, and motion in these parts, in obedience to the natural stimulus, becomes impossible. But, while we cannot induce generation of nerve-force in the centres by the direct application of any agent to them, this force may be imitated by stimulation applied to the nerve itself. A nerve that will respond to direct stimulation is said to be excitable; but this property does not extend throughout the entire conducting motor system. For example, we shall see when we come to study the properties of the encephalon, that certain fasciculi capable of conducting the motor stimulus from the centres to the muscles are not affected by direct stimulation, and seem to be inexcitable.

If a motor nerve be divided, galvanic, mechanical, or other stimulation applied to the extremity connected with the centres produces no effect; but the same stimulation applied to the extremity connected with the muscles is followed by contraction. The phenomena indicating that a nerve retains its physiological properties are always manifested at its peripheral distribution, and do not essentially vary when the nerve is stimulated at different points in its course. For example, stimulation of the anterior roots near the cord produces contraction in those muscles to which the fibres of these roots are distributed; but the same effect follows stimulation of the nerve going to these muscles in any part of its course.

As far as their physiological action is concerned, the different nerve-fibres are entirely independent, and the relations which they bear to each other in the nervous fasciculi and in the so-called anastomoses of nerves involve simple contiguity. If we compare the nerve-force to galvanism, each individual fibre seems completely insulated; and a stimulus conducted by it to muscles never extends to the adjacent

fibres. That it is the axis-cylinder which conducts and the medullary tube which insulates, it is impossible to say with positiveness; but, as we have already seen, it is more than probable that the central band is the only conducting element.

We have incidentally noted the fact that direct stimulation applied to the centres, even when the connection between these and the muscles is perfect, is incapable of inducing the generation of nerve-force; but the generation of a motor stimulus may be induced by an impression made upon sensitive nerves and conveyed by them to the centres. If, for example, we isolate a certain portion of the central nervous system, as the spinal cord, and leave its connections with the motor and sensitive nerves intact, these phenomena may be readily observed: An impression made upon the sensitive nerves will be conveyed to the gray matter of the cord and will induce the generation of a motor stimulus by the cells of this part, which will be conducted to the muscles and give rise to contraction. As the stimulus, in such observations, seems to be reflected from the cord through the motor nerves to the muscles, this action has been called reflex. These phenomena constitute an important division in the physiology of the nervous system, and will be fully considered by themselves.

Associated Movements.—It is well known that the action of certain muscles is with difficulty isolated by an effort of the will. This applies to sets of muscles on one side of the body and to corresponding muscles upon the two sides. For example, it is almost impossible, without great practice, to move some of the fingers, restraining the movements of the others; and the action of certain sets of muscles of the extremities is always simultaneous. The toes, which are but little used as the foot is confined in the ordinary dress, are capable of very little independent action. It is difficult to move one eye without the other, or to make rapid rotary

movements of one hand, while an entirely different order of movements is executed by the other; and instances of this kind might be multiplied.

In studying these associated movements, the question arises as to how far they are due to the anatomical relations of the nerves to the centres and their connections with muscles, and how far they depend upon habit and exercise. We can imagine that there are certain sets of nerve-cells, connected with each other by commissural fibres and giving origin to motor nerves distributed to sets of muscles; an anatomical arrangement that might render a separate action of these cells impossible. The anatomy of the nerve-centres and their connection with fibres are so difficult of investigation, that demonstrative proof of the existence of such systems is impracticable; but this affords a ready explanation of the fact that we cannot, as a rule, by an effort of the will, cause a portion only of a single muscle to contract; yet some of the larger muscles receive an immense number of motor nerve-fibres which are probably connected with gray matter composed of numerous anastomosing cells.

Many of the associated movements are capable of being influenced to a surprising degree by education, of which no better example can be found than in the case of skilful performers upon certain musical instruments, such as the piano, harp, violin, and other stringed instruments. In the technical study of such instruments, not only does one hand become almost independent of the other, but very complex associated movements may be acquired. An accomplished pianist or violinist executes the different scales automatically by a single effort of the will, and frequently pianists execute at the same time scales with both hands, the action being entirely opposed to the natural association of movements. Feats of sleight of hand also show how wonderfully the muscles may be educated, and to what an extent the power of association and disassociation of movements may be acquired by long practice.

Looking at the associated movements in their relations to the mode of action of the motor nerves, it seems probable that, as a rule, the anatomical relations of the nerves are such that a motor stimulus, or an effort of the will, cannot be conducted to a portion only of a muscle, but must act upon the whole muscle, and the same is true, probably, of certain restricted sets of muscles; but the association of movements of corresponding muscles upon the two sides of the body, with the exception, perhaps, of the muscles of the eyes, is due mainly to habit, and may be greatly modified by education.

Mode of Action of the Sensory Nerves.—The sensory nerve-fibres, like the fibres of the motor system, are entirely independent of each other in their action; and in the so-called anastomoses that take place between sensory nerves, the fibres assume no new relations, except as regards contiguity.

As motor fibres convey to their peripheral distribution the stimulus engendered by an irritation applied in any portion of their course, so an impression made upon a sensitive nerve is always referred to the periphery. A familiar example of this is afforded by the very common accident of contusion of the ulnar nerve as it passes between the olecranon and the condyle of the humerus. This is attended with painful tingling of the ring and little finger and other parts to which the filaments of this nerve are distributed, without, necessarily, any pain at the point of injury. More striking examples are afforded in neuralgic affections dependent upon disease or pressure on the trunk of a sensitive nerve. In such cases, excision of the nerve is often practised, but no permanent relief follows unless the section be made between the affected portion of the nerve and the nerve-centres; and the pain produced by the disease is always referred to the termination of the nerve, even after it has been divided between the seat of the disease and the periphery,

leaving the parts supplied by the nerve insensible to direct irritation. In cases of disease it is not unusual to note great pain in parts of the skin that are insensible to direct impressions.[1] The explanation of this is, that the nerves are paralyzed near their terminal distribution, so that an impression made upon the skin cannot be conveyed to the sensorium; but that the trunks of the nerves still retain their conducting power and are the seat of diseased action, producing pain, which is referred by the patient to the periphery.

In multiplying examples showing the mode of action of the sensory nerves, we may refer to the sensations experienced after certain plastic operations. In the very common operation of restoring the nose by transplanting skin from the forehead, after the operation has been completed, the skin having been entirely separated and cicatrized in its new relations, the patient feels that the forehead is touched when the finger is applied to the artificial nose. After a time, however, the sensorium becomes accustomed to the new arrangement of the parts, and this deceptive feeling disappears.

There are certain curious nervous phenomena, that are not without physiological interest, presented in persons who have suffered amputations. It has been long observed that after loss of a limb the sensation of the part remains and pain is frequently experienced referred to the amputated member. Thus a patient will feel distinctly the fingers or toes after an arm or a leg has been removed, and irritation of the ends of the nerves at the stump produces sensations referred to the missing member. A few years since, we observed a very striking example of this in a soldier who had suffered amputation of the leg. While this patient was walking about on crutches, before the stump had entirely healed, on getting up suddenly from his seat, he attempted to walk, and put the stump to the ground, producing considerable injury. His explanation was, that he felt the foot perfectly, and it was

[1] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 178.

necessary for him to be constantly on his guard to prevent such an accident.

A very curious fact has been observed with regard to the imaginary presence of limbs after amputation, which we have had ample opportunities of verifying. After a time the sense of possession of the lost limb becomes blunted, and may, in some cases, entirely disappear. This may take place a few months after the amputation, or the sensations may remain in their full intensity for years. Examples are reported by Müller where the sense was undiminished thirteen, and, in one case, twenty years after amputation.[1] In a certain number of cases, however, the sense of the intermediate part is lost, the feeling in the hand or foot, as the case may be, remaining as distinct as ever, the impression being that the limb is gradually becoming shorter. These curious facts, noted by M. Gueniot,[2] show that the sense of the limb becoming shorter is observed in about half of the cases of amputation in which cicatrization goes on regularly; and in these cases, the patient finally experiences a feeling as though the hand or foot were in direct contact with the stump. By careful inquiries among a large number of patients in military hospitals, we have been enabled to verify these observations in the most satisfactory manner.

[1] Müller, *Elements of Physiology*, London, 1840, vol. i., p. 746.

[2] Gueniot, *D'une hallucination du toucher (ou hétérotophie subjective des extré mités) particulière à certains amputés.—Journal de la physiologie*, Paris, 1861, tome iv., p. 416, *et seq.*

CHAPTER III.

GENERAL PROPERTIES OF THE NERVES.

Nervous irritability—Different means employed for exciting the nerves—Disappearance of the irritability of the motor and sensory nerves after exsection—Nerve-force—Non-identity of nerve-force with electricity—Rapidity of nervous conduction—Estimation of the duration of acts involving the nerve-centres—Action of electricity upon the nerves—Contrasted action of the direct and the inverse current on closing and opening the circuit—Voltaic alternations—Induced muscular contraction—Galvanic current from the exterior to the cut surface of a nerve—Effects of a constant galvanic current upon the nervous irritability—Electrotonus, anelectrotonus, and cathelectrotonus—Neutral point—Negative variation.

Numerous experiments have been made, especially upon the cerebro-spinal nerves, with regard to their action under different kinds of stimulation, the probable nature of the nervous agent, or nerve-force, the extent and duration of their excitability and sensibility, etc., which have developed facts of more or less physiological interest and importance. As far as the nerves of general sensibility are concerned, the phenomena of conduction of impressions are essentially the same in all, if we except certain variations in different nerves as regards the degree of sensibility. The motor nerves all respond in the same manner to stimulation; and it is upon this portion of the nervous system that the most important observations have been made. This being the case, it is evident that the cerebro-spinal nerves, in their behavior under the experimental conditions above enumerated, possess certain general properties, and that the functions of special nerves are to be studied, after a full consideration

of these general properties, in connection with their anatomical distribution to the different organs in the economy.

The points to be considered, aside from the simple division of the nerves into motor and sensory, are as follows:

1. The conditions of excitability and sensibility of the nerves, or what is known as nervous irritability.

2. The nature of the nervous agent, or the so-called nerve-force.

3. Certain phenomena following the application of electricity to the nerves.

Nervous Irritability.—We have already alluded in a general way to what is known as nervous irritability.[1] The term is used by physiologists to express the condition of nerves which enables them to respond to artificial stimulation, or to conduct the natural stimulus or external impressions. So long as a nerve retains this property it is said to be irritable. Of course, while in a normal condition and during life, irritability, as applied to nerves, simply means that these parts are capable of performing their peculiar functions; but, after death, for a certain time the nerves will respond to artificial stimulation; and it is to this property that the term "irritability" seems to be most applicable. At a certain time after death, varying in different classes of animals with the activity of their nutrition, the irritability of the nerves disappears. This occurs very soon in warm-blooded animals, but is later in animals lower in the scale, so that the latter present the most favorable conditions for experimentation. Most observations on nervous irritability, indeed, have been made upon frogs and other cold-blooded animals. Analogous facts have already been noted with regard to the muscular system, although, as we have seen, the irritability of the muscular tissue is entirely distinct from that of the nerves.[2]

Immediately or soon after death, when the irritability of

[1] See page 66. [2] See vol. iii., Movements, p. 464.

the nerves is at its maximum, they may be excited by mechanical, chemical, or galvanic stimulus, all of these agents producing contraction of the muscles to which the motor filaments are distributed. Mechanical irritation, simply pinching a portion of the nerve, for example, produces a single muscular contraction; but if the injury to the nerve be such as to disorganize its fibres, that portion of the nerve will no longer conduct a stimulus. Among the irritants of this kind, we may cite the extremes of heat and cold. If an exposed nerve be cauterized, a vigorous muscular contraction follows. The same effect, though less marked, may be produced by the sudden application of intense cold. Among chemical reagents, there are some that excite the nerves and others which produce no effect; but these are not important from a physiological point of view. Suffice it to say that mechanical irritation and the action of certain chemicals are capable of exciting the nerves; but that when their action goes so far as to disorganize the fibres, the conducting power of these fibres is lost. While, however, irritation of the nerve above the point of injury has no effect, stimulation between this point and the muscles is still followed by contraction.

The most convenient method of exciting the nerves in physiological experiments is by means of electricity, a stimulus more closely resembling the nerve-force than any other, and one which may be employed without disorganizing the nerve-tissue, and consequently admits of extended and repeated application. The action of electricity, however, with the methods of preparing the nerves and muscles for experimentation, will be fully considered under a separate head.

The irritability of the motor system is entirely distinct from that of the sensory nerves, and one may be destroyed, leaving the other intact. This follows almost as a matter of course upon the fact of the anatomical distinction between motor and sensory nerves; but it is interesting to note the limits of the irritability after death in nerves of different

properties and the differences in the manner of its disappearance. The woorara-poison, a very curious agent prepared by the South-American Indians, has the remarkable property of paralyzing the motor nerves, leaving the nerves of sensation intact. This fact has been demonstrated by Bernard and others by very curious and ingenious experiments. The poison, like those of animal origin, acts most vigorously after introduction under the skin or absorption from wounds, and produces no toxic effects when taken into the stomach, except when introduced in large quantity in fasting animals. Under the influence of this agent, an animal dies with complete paralysis of the motor system, presenting, among other phenomena, arrest of respiration. Most of the varieties of the poison affect only the motor nerves, and do not influence the action of the heart; and in animals brought completely under its influence, artificial respiration will enable the heart to continue its action, and, in some instances, if this be persisted in, recovery will take place.

The fact that the woorara-poison affects the motor nerves only has been experimentally illustrated by Bernard, taking advantage of the reflex functions of the spinal cord to show the persistence of the irritability of the sensory nerves. The most striking of these experiments is the following: A frog is prepared by exposing the nerves in the lumbar region, and then isolating the posterior extremities by applying a strong ligature, including the aorta and all the parts except the nerves; so that, practically, the only communication between the posterior extremities and the body is by the nerves. It is evident, therefore, that if the poison be introduced under the skin of the body, acting, as it does, through the blood, it will affect all parts except the posterior extremities; for the poison acts from the periphery to the centres, and must circulate in the parts to which the motor nerves are distributed. If the posterior extremities be now irritated, the impression is conveyed to the spinal cord through the sensory filaments of the lumbar nerves,

which are intact; this gives rise to a stimulus, which is reflected back through the motor filaments of the same nerve, and the ordinary reflex movements are observed in the posterior extremities. This is to be expected, inasmuch as the posterior extremities are removed from the influence of the poison. If the anterior extremities, which are completely under the influence of the poison, be now irritated, no movements are observed in these parts, but they take place, as before, in the posterior extremities. The mechanism of this action is easily understood. Reflex phenomena, consisting in the movements of muscles, may be manifested throughout the entire system, following irritation of a single part. An impression made upon the surface is conveyed to the spinal cord, and, if this be sufficiently powerful, motor stimulus may be sent through all of the anterior roots coming from the cord. The impression made upon the anterior, or poisoned extremities, is conveyed by the sensory filaments to the cord and is transmitted to the posterior extremities through their motor nerves, which are intact. The fact of the transmission of the impression from the anterior extremities to the cord shows that the poison does not affect the sensory system.[1]

In the same way that the woorara-poison paralyzes the motor nerves, leaving the sensory system intact, other agents, as anæsthetics, will abolish the sensibility of the nerves without affecting the motor filaments. This well-known fact has also been experimentally illustrated by Bernard.[2]

As we have already intimated in another connection, the nerves soon lose their irritability after they have been separated from the centres.[3] This loss of conducting power is

[1] BERNARD, *Leçons sur la physiologie et la pathologie du système nerveux*, Paris, 1858, tome i., p. 203, *et seq.*; and, *Leçons sur les propriétés des tissus vivants*, Paris, 1866, p. 254, *et seq.*

[2] BERNARD, *Théorie physiologique de l'anesthésie.—Revue des cours scientifiques*, Paris, 1868–'69, tome vi., p. 383.

[3] See page 80.

attended with important structural changes in the nerve-fibres. The tubes lose their normal appearance, and the medullary matter becomes opaque and coagulates in large drops. The axis-cylinder is not so much modified in structure, but it certainly loses its characteristic physiological properties.

The excitability of the motor nerves, according to the observations of Longet, disappears in about four days after resection.[1] Of course, in experiments upon this point, it is necessary to excise a portion of the nerve to prevent reunion of the divided extremities; but when this is done, after the fourth day, galvanization of the nerve will produce no contraction in the muscles, though the latter retain their contractility, as may be shown by the application of direct irritation. This loss of irritability is gradual, and continues, whether the nerve be exposed and stimulated from time to time or be left to itself; and the loss of excitability progresses from the centres to the periphery. In the researches of Longet on this subject, it was found that the lower portion of the peduncles of the brain lost their irritability first; then the anterior columns of the cord, then the motor roots of the nerves, and, last of all, the branches of the nerves near their termination in the muscles.

The sensibility of the sensory nerves disappears from the periphery to the centres, as is shown in dying animals and in experiments with anæsthetics. The sensibility is lost, first in the terminal branches of the nerves, next in the trunks and in the posterior roots of the spinal nerves, and so on to the centres.[2] We have often illustrated this fact in experiments upon the roots of the spinal nerves and in section of the large root of the fifth pair within the cranial cavity. When an animal is brought so completely under the influence of ether that the operation of opening the spinal canal may be performed without inflicting the slightest

[1] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 171.

[2] LONGET, *op. cit.*, p. 175.

pain, the posterior roots will be found to be distinctly sensible. We have lately been in the habit, in class-demonstrations, of dividing the fifth pair in the cranium without using an anæsthetic, as the operation is instantaneous and the effects are much more striking in this way; but when we have used an anæsthetic, we could never push the effects sufficiently to abolish the sensibility of the root of the nerve. In an animal brought so fully under the influence of ether that the conjunctiva, supplied with branches of the fifth, had become absolutely insensible, the instant the instrument touched the root of the nerve in the cranium, there were evidences of acute pain. Nothing could more strikingly illustrate the mode of disappearance of the sensibility of the nerves from the periphery to the centres.

The nervous irritability may be momentarily destroyed by severe shock in killing an animal. This is sometimes illustrated in preparing frogs for experiments on the nerves; the shock of killing the frog by decapitation, tearing off the skin, etc., abolishing the irritability of the nerves for the moment. The observations of Longet and Masson have shown, also, that a galvanic shock sufficiently powerful to destroy life abolishes instantly the excitability of the motor nerves.[1]

Nerve-Force.—The so-called nervous irritability, artificially manifested by the application of a stimulus directly to the nerve-tissue, enables the nerves to conduct from the centres to the periphery a force which is generated in the gray substance. This we may call the nerve-force. Its production is one of the most remarkable of the phenomena of life; and its essence, or the exact mechanism of its generation, is one of the problems that has thus far eluded the investigations of physiologists. We know, however, that in the operations of the nervous system, the nerves serve simply as conductors and the nerve-cells generate the nerve-

[1] Longet, *Traité de physiologie*, Paris, 1869, tome ii., p. 602.

force. It is evident, also, that nearly all of the so-called vital phenomena are more or less influenced and controlled through this wonderful agent; and throughout our study of the nervous system, we shall be constantly investigating the phenomena attending the operation of nerve-force, while compelled to admit our ignorance of its essential nature.

Non-identity of Nerve-Force with Electricity.—When we come to study fully the action of electricity upon the nerves, we shall see that this is by far the most convenient stimulus for exciting the nervous action, and one by which we closely imitate the true nerve-force. So great is the similarity, indeed, between some of the phenomena produced by the application of electricity and those attending the physiological action of nerves, that some physiologists have regarded the nerve-cells as generators of an electric current. This hypothesis explains the nature of nerve-force, in so far as it assimilates it to a force, with the action of which, as artificially generated, we are more or less familiar. No one at the present day, however, pretends that the nerve-force has been demonstrated to be identical with any form of electricity; and the question does not now demand extended discussion.

A series of experiments made by Prévost and Dumas, in 1823, are worthy of note as showing the absence of a true electric current in nerves in action;[1] but these have been confirmed in later years with apparatus sufficiently delicate to settle the question beyond a doubt. The most conclusive experiments on this subject are those of Matteucci and Longet, made upon horses at the veterinary school at Alfort. These physiologists exposed the sciatic nerves in the living

[1] Prévost et Dumas, *Mémoire sur les phénomènes qui accompagnent la contraction de la fibre musculaire.—Journal de physiologie*, Paris, 1823, tome iii., p. 328. Analogous experiments, with the same results, were made later by Person (*Sur l'hypothèse des courans électriques dans les nerfs.—Journal de physiologie*, Paris, 1830, tome x., p. 216, *et seq.*).

animal, and, when there was evidently a conduction in both directions, as evinced by pain and muscular action, failed to detect the slightest evidence of an electric current with the most delicate galvanometer that could be constructed. The fact of the absence of a galvanic current in nerves during their physiological action was even more strikingly illustrated by Matteucci, who demonstrated, in the electric eel, that although the electric discharges from the peculiar organs of this animal were under the control of the nervous system, and could be excited by galvanic stimulation of the proper nerves immediately after death, no galvanic current existed in these nerves during their physiological action.[1]

When we abandon the hypothesis of the identity of nerve-force with electricity, we are compelled to admit that the agent generated by the nerve-centres is *sui generis*, and not to be compared with any force generated outside of living organisms or artificially produced by direct stimulation of the nerves; but we admit, nevertheless, the fact that electricity may be generated by animals, as the electric fishes, and that electric currents exist in different anatomical elements of the living body, including the nerves, under certain conditions. Our study of the nerve-force, then, leaving its essential nature unexplained, is mainly confined to a description of its attending phenomena.

Rapidity of Nervous Conduction.—Until within the last few years, it has been assumed by many that the rapidity of nervous conduction was one of those problems in human physiology that could never be satisfactorily resolved; and those who have investigated the history of this question, which dates from before the time of Haller, have often quoted the words of Müller, who says, in his great work on the "Elements of Physiology," that "we shall probably never attain the power of measuring the velocity of nervous action; for we have not the opportunity of comparing its

[1] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 276, *et seq.*

propagation through immense space, as we have in the case of light."[1]

The conjectures of writers before Haller were based upon the supposed similarity between nervous conduction and the passage of electricity; but Haller formed an estimate of the rapidity of nervous conduction by ascertaining the number of letters he was able to pronounce in one minute in reading aloud from the "Æneid."[2] Calculating then the distance of the nervous course from the brain to the muscles, he estimated that the nerve-force moved at the rate of about one hundred and fifty feet in a second.[3] This estimate is not very far from the truth; at all events, it gives an idea of the relative slowness of nerve-conduction as compared with electricity or light, which travels at the rate of many hundred millions of feet in a second.

The first rigorous estimates of the velocity of the nerve-current were made in 1850, by Helmholtz,[4] and were applied to the motor nerves. The important and interesting results of these experiments were arrived at by an ingenious application of the graphic method, which has since been so largely improved and extended by Marey, and their accuracy was rendered possible by the exceedingly delicate chronometric apparatus which has been devised within the last few years.

It is unnecessary to describe fully the exact methods employed by Helmholtz and those who immediately followed in his investigations; suffice it to say that this distinguished physiologist and physicist constructed apparatus which, though somewhat complex, was so accurate as to leave no doubt as to the reliability of his results. Taking into account all of the disturbing conditions, and allowing for the

[1] Müller, *Elements of Physiology*, London, 1840, vol. i., p. 729.

[2] Haller, *Elementa Physiologiæ*, Lausannæ, tomus iv., p. 483.

[3] *Op. cit.*, tomus iv., p. 373.

[4] Helmholtz, *Note sur la vitesse de propagation de l'agent nerveux dans les nerfs rachidiens.—Comptes rendus*, Paris, 1850, tome xxx., p. 204, and, 1851, tome xxxiii., p. 262.

interval of *pose*, or the length of time between the excitation of a muscle and the commencement of its contraction,[1] he estimated the rapidity of conduction in the motor nerves of the frog at about eighty-five feet per second.[2] The results obtained by Marey upon frogs give a much slower rate of nervous conduction. These were followed, however, by the observations of Helmholtz and Baxt on the human subject, which are, of course, the most interesting of all.

The process devised by Marey is beautifully simple. He employed, to estimate small fractions of a second, a cylinder graduated in the following manner: An ordinary tuning-fork, vibrating, say, five hundred times per second, is so arranged that a point connected with one of its arms is made to play against a strip of blackened paper. As the paper remains stationary, the point makes but a single mark; but when the paper moves, as the point vibrates, a line is produced with regular curves, every curve representing $\frac{1}{500}$ of a second. Now, if a lever be attached to a muscle, and be so arranged as to mark upon the paper, moving at the same rate, the instant when contraction takes place, it is evident that the interval between two contractions produced by stimulating the nerve at different points of its course will be most accurately indicated; and if the length of the nerve between the two points of stimulation be known, the difference in time will represent the rate of nervous conduction.[3]

In experiments upon frogs, the leg is prepared by cutting away the muscles and bone of the thigh, leaving the nerve attached. The lever is then applied to the muscles of the leg and the stimulation is applied successively at two points in the nerve, the distance between them being carefully measured. The results obtained in this way showed a rate

[1] See vol. iii., Movements, p. 472.

[2] *Comptes rendus*, Paris, 1851, tome xxxiii., p. 262.

[3] Marey, *Du mouvement dans les fonctions de la vie.—Revue des cours scientifiques*, Paris, 1865–'66, tome iii., p. 346, *et seq.;* and, *Du mouvement*, etc., Paris, 1868, p. 410, *et seq.*

of conduction of from thirty-six to forty-six feet per second; but these are not regarded by Marey as invalidating the estimates by Helmholtz, in view of the various conditions by which the rapidity of conduction is modified.[1]

Employing the myograph of Marey, Baxt, in the laboratory of Helmholtz, has succeeded in measuring the rate of nervous conduction in the human subject. In these experiments, the swelling of the muscle during contraction was limited by enclosing the arm in a plaster-mould, and noting the contraction through a small opening. By then exciting the contraction by stimulating the radial nerve successively at different distances from the muscle, the estimate was made. The rate in the human subject was thus estimated at one hundred and eleven feet per second.[2] The latest experiments on this subject by Helmholtz and Baxt, in which great care was taken in the adjustment of the apparatus, showed a mean of rapidity for the motor nerves, in man, of about two hundred and fifty-four feet per second. These observations were made in the summer of 1869; and the difference in the results is in part explained by the fact, which was ascertained experimentally at that time, that a high temperature increases, and a diminished temperature retards the velocity of nervous conduction.[3] It has been further shown by Munk, that the rate of conduction is different in different portions of the nervous trunk; the rapidity progressively increasing as the nerve approaches its termination.[4]

Helmholtz, Du Bois-Reymond,[5] Marey, and others, have

[1] Marey, *Du mouvement*, etc., Paris, 1868, p. 433.

[2] Baxt, *Versuche über die Fortpflanzungsgeschwindigkeit der Reizung in den motorischen Nerven des Menschen.—Monatsberichte der königlich Preussischen Akademie der Wissenschaften zu Berlin, aus dem Jahre*, 1867, Berlin, 1868, S. 233.

[3] Helmholtz und Baxt, *Fortpflanzungsgeschwindigkeit der Erregung in Bewegungsnerven.—Der Naturforscher*, Berlin, 1870, Bd. iii., S. 230.

[4] Munk, *Untersuchungen über die Zeitung der Erregung in Nerven.—Archiv für Anatomie, Physiologie, und wissenschaftliche Medecin*, Leipzig, 1864, S. 798, *et seq.*

[5] Du Bois-Reymond, *Vitesse de la transmission de la volonté et de la sensation à travers les nerfs.—Revue des cours scientifiques*, Paris, 1866–'67, tome iv., p. 37

noted certain conditions which modify the rate of nervous conduction. One of the most prominent of these, first observed by Helmholtz, is due to modifications in temperature. By a reduction of temperature, in the frog at least, the rate is very much reduced; and at 32° it is not more than one-tenth as rapid as at 60° or 70°. Marey has also noted that the rate is sensibly reduced by fatigue of the muscles.[1]

The same principle which has led to the determination of the rate of conduction in motor nerves; viz., an estimation of the difference in time of the passage of a stimulus applied to a nerve at two points situated at a known distance from each other, has been applied to the conduction of sensations. Hirsch is quoted as having made the first attempt to resolve this question, in 1851.[2] He employed the delicate chronometric instruments used in astronomy, and noted the difference in time between the appreciation of an impression made upon a part of the body far removed from the brain, as the toe, and an impression made upon the cheek. This process admitted of the rough estimate of about one hundred and eleven feet per second; an estimate agreeing remarkably with that of Baxt for the motor nerves. The later and more elaborate researches of Schelske show a rapidity of conduction by the sensory nerves of about ninety-seven feet per second.[3]

Attempts have been made by Helmholtz, Du Bois-Reymond,[4] Marey,[5] Donders,[6] and others, to estimate the dura-

[1] MAREY, *Du mouvement dans les fonctions de la vie*, Paris, 1868, p. 433.

[2] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 291.

[3] SCHELSKE, *Neue Messungen der Fortpflanzungsgeschwindigkeit des Reizes in den menschlichen Nerven.—Archiv für Anatomie, Physiologie und wissenchaftliche Medecin*, Leipzig, 1864, S. 172.

[4] DU BOIS-REYMOND, *On the Time required for the Transmission of Volition and Sensation through the Nerves. A Lecture given at the Royal Institution.*—BENCE JONES, *Croonian Lectures on Matter and Force*, London, 1868, Appendix I., p. 97, *et seq.*; and, *Revue des cours scientifiques*, Paris, 1866–'67, tome iv., p. 39, *et seq.*

[5] MAREY, *Du mouvement dans les fonctions de la vie*, Paris, 1868, p. 442.

[6] DONDERS, *Velocity of Cerebral Functions.—The Quarterly Journal of Psychological Medicine*, New York, 1869, vol. iii., p. 763, *et seq.*

tion of acts involving the central nervous system, as the reflex phenomena of the spinal cord or the operations of the cerebral hemispheres. These have been partially successful, or, at least, they have shown that the reflex and cerebral acts require a distinctly appreciable period of time. This, in itself, is an important fact; though the duration of these acts has not yet been measured with all the accuracy that could be desired. As the general result of experiments upon these points, it is found that the reflex action of the spinal cord occupies more than twelve times the period required for the transmission of stimulus or impressions through the nerves.[1] Donders found, in experiments on his own person, that an act of volition required one-twenty-eighth of a second, and one of simple distinction or recognition of an impression, one-twenty-fifth of a second.[2] These estimates, however, are merely approximative; and until they attain greater certainty, it is unnecessary to describe in detail the apparatus employed.

The general result of the various observations we have detailed upon the rate of nervous conduction as applied to the human subject is, in the first place, that this can be measured with tolerable accuracy; second, that it is in no wise to be compared with the rate of conduction of light or electricity; and, finally, that the rate in the human subject is essentially the same in the motor and sensory nerves, being, according to the most reliable estimates, about one hundred and eleven feet per second.

Elevation of Temperature in Nerves during their Functional Activity.—There is little to note under this head, except the fact that functional activity of the nerves produces an amount of elevation to temperature in their substance which can be distinctly demonstrated by sufficiently delicate thermometric apparatus. Under the head of animal heat, in another volume, we have given the results of recent ob-

[1] Du Bois-Reymond, *loc. cit.*

[2] Donders, *loc. cit.*

servations by Lombard, showing an elevation in the temperature of the head during mental exertion.[1] The same facts have lately been observed by Schiff,[2] who has also shown a slight elevation of temperature in nerves during the conduction of an artificial stimulus.[3]

Action of Electricity upon the Nerves.—A great deal has been written upon the effects of electricity upon the nervous system, and facts elicited by experiments upon this subject are highly important in their bearing on physiology and pathology. Still, there are numerous observations upon this subject which have but little importance, in a purely physiological sense, except that they are curious and interesting. These we do not propose to discuss elaborately; but shall confine ourselves chiefly to those points which bear directly upon our knowledge of the properties and functions of the nerves.

The first important fact—to which we have already alluded—is, that electricity is the best means that we have of artificially exciting the nerves. Using electricity, we can regulate with exquisite nicety the degree of stimulation; we can excite the nerves long after they have ceased to respond to mechanical or chemical irritation; the effects of different currents can be noted; and, finally, this mode of stimulation produces a peculiar and interesting condition of the parts of the nerve not included between the poles of the battery. For these reasons, it seems proper to devote some consideration, in this connection, to the effects of the application of this agent to the nerves.

So long as the nerves retain their irritability, they will respond to an electrical stimulus. Experiments may be made upon the exposed nerves in living animals or in ani-

[1] See vol. iii., Animal Heat, p. 415.

[2] MORITZ SCHIFF, *Recherches sur l'échauffement des nerfs et des centres nerveux à la suite des irritations sensorielles et sensitives.*—*Archives de physiologie*, Paris, 1870, tome iii., p. 5, *et seq.*

[3] Ibid., 1869, tome ii., pp. 157 and 330.

mals just killed; and, of all classes, the cold-blooded animals present the most favorable conditions, an account of the persistence of nervous and muscular irritability for a considerable time after death. Experimenters most commonly use frogs, on account of the long persistence of the irritability of their tissues and the facility with which certain portions of the nervous system can be exposed. For ordinary experiments upon the nervous conduction, the parts are prepared by detaching the posterior extremities, removing the skin, and cutting away the bone and muscles of the thigh, so as to leave the leg with the sciatic nerve attached. A frog's leg thus isolated presents a nervous trunk one or two inches in length, attached to the muscles, which will respond to the slightest stimulus. It is by experiments made upon frogs prepared in this way that most of the important facts relative to the action of electricity upon the nervous system have been developed.

It is evident that the galvanic current may be applied to a nerve so that the direction may, in the one case, follow the course of the nerve, that is, from the centre to the periphery, and, in the other, be opposite to the course of the nerve. These currents have been called respectively the direct, or descending, and the inverse, or ascending.[1] When the positive pole (the copper) is placed nearer the origin of the nerve, and the negative pole (the zinc) below this point in the course of the nerve, the galvanic current follows the normal direction of the motor conduction, and this is called the direct current. When the poles are reversed, and the direction of the galvanic current is from the periphery toward the centre, it is called the inverse current. It will be convenient to speak of these two currents respectively as direct and inverse, in detailing experiments upon the action of electricity upon the nerves.

The points to be noted with regard to the effects of the

[1] The direct current is sometimes called centrifugal, and the inverse, centripetal.

application of electricity to an exposed nerve are the action of constant currents of different degrees of intensity, the phenomena observed on making and breaking the circuit, and the effects of an interrupted current.

During the passage of a feeble constant current through an exposed nerve, whatever be its direction, there are no convulsive movements and no evidences of pain. This fact has long been recognized by physiologists, who at first limited the effects of electricity upon the nerves to two periods, one at the making of the circuit and the other at its interruption. We shall see, however, that the passage of electricity through a portion of a nervous trunk produces a peculiar condition in parts of the nerve not included between the poles of the battery, described by Du Bois-Reymond under the name of electrotonus; but the fact that neither motion nor sensation is excited in a mixed nerve during the actual passage of a feeble constant current is not invalidated.

If a sufficiently powerful constant current be passed through a nerve, disorganization of its tissue takes place, and the nerve finally loses its excitability, as it does when bruised, ligatured, or when its structure is destroyed in any other way.[1] It was thought by Galvani, and the idea has been adopted by Matteucci, Guérard, and Longet,[2] that a current directed exactly across a nerve, so as to pass at right angles to its fibres, does not give rise to muscular contraction; but it is doubtful whether this can be accepted as a demonstrated fact. Chauveau has found that a transverse current passed through the exposed facial nerve of a horse produces well-marked muscular action. He is of the opinion that the experiments of Galvani and his followers, made upon frogs, are faulty, inasmuch as the nerve is so small that but little if any of the galvanic current passes through its substance, being conducted from one pole to the other through

[1] BERNARD, *Leçons sur la physiologie et la pathologie du système nerveux*, Paris, 1858, tome i., p. 162.

[2] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 193.

the surrounding moisture, which, in his own experiments, was carefully removed.[1] Longet has noted that pain is produced by the passage of a transverse current through a sensitive trunk, and that the pain does not seem to be increased when the poles are separated and the current thus is sent through a portion of the length of the nerve.[2]

All who have experimented upon the action of galvanism upon the mixed nerves have noted the fact alluded to above, that the phenomena of contraction are manifested only on closing or breaking the circuit. Take, for example, a frog's leg prepared with the nerve attached; place one pole of a feeble galvanic apparatus on the nerve and then make the connection, including a portion of the nerve in the circuit, and usually, a contraction of the muscles will occur when the circuit is closed, the limb will be quiet during the passage of the current, and another contraction will take place when the circuit is broken. When the parts are freshly prepared, the contractions take place as described, whatever be the direction of the current.[3] After a time, however, the nervous irritability becomes somewhat enfeebled, and then it is observed that the contraction occurs in some instances when the circuit is closed, and in others when the circuit is broken. The differences in the time of appearance of these phenomena have been found to depend upon the direction of the current, and may be formularized as follows:

If the sciatic nerve attached to the leg of a frog, prepared

[1] CHAUVEAU, *Effets physiologiques de l'électricité.—Journal de la physiologie*, Paris, 1860, tome iii., p. 298.

[2] LONGET, *loc. cit.*, p. 201.

[3] A form of galvanic apparatus which we have long used and found very convenient for these experiments is essentially the one described by Bernard (*Système nerveux*, Paris, 1858, tome i., p. 144). It consists simply of alternate copper and zinc wires wound around a piece of wood bent in the form of a horseshoe and terminating in two platinum points representing the positive and negative poles. This forms a sort of electric forceps, about eight inches long, which, when moistened with water slightly acidulated with acetic acid, will give a current of about the strength required for most of the experiments detailed above.

in the usual way for such experiments, be subjected to a feeble galvanic current, there is a time when muscular contraction takes place only at the instant when the circuit is made; no contraction occurring when the circuit is broken; and this occurs only with the direct current; i. e., when the current flows toward the periphery, the positive pole being above, and the negative below. If the poles be reversed, so that the galvanic current flows from the periphery toward the centres—the inverse current—contraction of the muscles occurs only when the circuit is broken and none takes place when the circuit is closed.

These phenomena are distinct after the irritability of the parts has become somewhat diminished by exposure or by electric stimulation of the nerve, but they may occur in perfectly fresh parts, when the galvanic current is very feeble. Usually, when the nervous irritability is at its height, contractions occur both on closing and breaking the circuit; but they are more powerful on closing the circuit, for the direct current, and on breaking the circuit, for the inverse current. This fact has been noted by all experimenters since the time of Ritter, by whom the essential characters of these phenomena were first described.[1] Ritter was in error in supposing an antagonistic action of the flexor and extensor muscles excited by making the circuit with the direct, and breaking the circuit with the inverse current; but most of his descriptions of the effects of different currents are remarkably accurate and have been fully confirmed by late observers.

A very simple experiment made by Matteucci strikingly illustrates the contrasted action of the direct and the inverse current. The posterior extremities of a frog are prepared so as to leave the nerves on the two sides connected together by a portion of the spinal column. The legs are then placed each one in a wineglass of water, and a feeble galvanic current is passed from one glass to the other. It is evident

[1] RITTER, *Beyträge zur nähern Kenntniss des Galvanismus*, Jena, 1805, Bd. ii., drittes, viertes und letztes Stück, S. 132, *et seq.*

that, with this arrangement, the current will pass through both nerves, being direct for the one and inverse for the other. In this case, if the irritability of the nerves be not too intense, there will be a contraction in the leg in which the current is direct at the time of making the circuit, while the other leg will contract when the circuit is broken.[1] This experiment has been modified by Chauveau, and applied to the two facial nerves in a living horse. A Leyden jar is very feebly charged with electricity, and the two facials are exposed. The current is then passed instantaneously through both the nerves, which gives but a single stimulus and that corresponds to the time of making the circuit with the constant current. In this experiment, the current is direct for one nerve and inverse for the other, and contraction takes place only in those muscles supplied with the nerve for which the current is direct.[2]

The muscular contraction produced by galvanic stimulation of the nerve is more vigorous the greater the extent of the nerve included between the poles of the battery. This fact has long been observed, and its accuracy is easily verified. It would naturally be expected that the greater the amount of stimulation the more marked would be the muscular action; and the stimulation seems to be increased in proportion to the extent of nerve through which the galvanic current is made to pass.

The irritability of a nerve, it is well known, may be exhausted by the repeated application of electricity, whatever be the direction of the current, and is more or less completely restored by repose. It is a curious fact, in this connection, that when the irritability of a nerve has been exhausted for the direct current, it will respond to the inverse current, and *vice versa*; and it is even more remarkable that after the irritability has been exhausted by the direct cur-

[1] MATTEUCCI, *Leçons sur les phénomènes physiques des corps vivants*, Paris, 1847, p. 233.

[2] CHAUVEAU, *op. cit.—Journal de la physiologie*, Paris, 1860, tome iii., p. 57.

rent, it is restored more promptly by stimulation with the inverse current than by absolute repose, and *vice versa.* This phenomenon, observed by Volta, is sometimes known as "voltaic alternation."[1] It is very strikingly illustrated in frogs prepared as above described, with the two posterior extremities, the nerves attached through a portion of the spinal cord, placed in vessels of water so that a current may be simultaneously passed through both nerves, being direct for the one and inverse for the other. As we have already seen, after a time, contraction occurs only in one leg, for which the current is direct, on making the circuit, and in the other, only on breaking the circuit. By repeatedly passing the current in this way, after a time there will be no contraction in either leg, the irritability of the nerves having become exhausted. If the poles of the battery be now reversed, so as to make the inverse current take the place of the direct, contractions with making and breaking the circuit will again occur. The irritability may again be exhausted and restored by changing the poles, and this may be repeated several times with the same preparation.

There can be no doubt with regard to the action of the direct and inverse currents, as above described, applied to nerves exclusively motor, as well as to the mixed nerves. In the mixed nerves separated from the centres, it is evident that the motor elements only are acted upon; and it would be difficult to understand how the action of these currents could be different when applied to the anterior roots of the spinal nerves. Longet and Matteucci, however, in their earlier experiments upon the anterior roots of the spinal nerves, observed that contraction of muscles took place on breaking the circuit, with the direct current, and on making the circuit, with the inverse current; precisely the opposite of the phenomena noted in experiments on the mixed nerves; and Longet proposed from this to draw a distinction between the ordinary nerves and those possessed of ex-

[1] Longet, *Traité de physiologie*, Paris, 1869, tome iii., p. 199.

clusively motor properties. The error in these observations, however, was early pointed out by Rousseau, whose experiments were fully detailed by Bernard before they were published separately.[1] Rousseau found that when galvanism was applied to a mixed nerve still connected with its centres, two galvanic currents were established; the one taking the shorter course through that portion of the nerve included between the poles of the battery, and the other, called the "derived current," taking an opposite direction through the nerves and the tissues. It is evident that the derived current would be inverse for the nerve when the shorter current is direct, and *vice versa.* Now if the extent of nerve included between the poles of the battery be short, the derived current would predominate, and we would seem to have contraction with the closure of the inverse and the opening of the direct current. This fact was fully demonstrated by Rousseau, who devised a little apparatus for neutralizing the derived current, when the phenomena following the application of the currents to the nerves attached were the same as those observed in divided nerves.[2] In 1859–'60, shortly after these experiments were published, we repeated them before a medical class, and have no doubt as to the accuracy of the results. The experiments of Rousseau have since been confirmed by Chauveau;[3] and Matteucci,[4] in his later publications, acknowledges the error of his first observations, though Longet still adheres to his original deductions.[5]

Induced Muscular Contraction.—A curious phenomenon

[1] Rousseau, in Bernard, *Leçons sur la physiologie et la pathologie du système nerveux*, Paris, 1858, tome i., p. 170, *et seq.*

[2] *Loc. cit.*, p. 181.

[3] Chauveau, *Effets physiologiques de l'électricité.—Journal de la physiologie*, Paris, 1860, tome iii., p. 458, *et seq.*

[4] Matteucci, *Phénomènes physico-chimiques des corps vivants.—Revue des cours scientifiques*, Paris, 1867–'68, tome v., p. 508.

[5] Longet, *Traité de physiologie*, Paris, 1869, tome iii., p. 187.

was discovered by Matteucci, in experimenting upon nervous and muscular irritability, which has been called "induced muscular contraction."[1] It was found that if the nerve of a galvanoscopic frog's leg (the leg prepared with the nerve attached in the way already described) be placed in contact with the muscles of another leg prepared in the same way, galvanization of the nerve giving rise to contraction of the muscles with which the nerve of the first leg is in contact will induce contraction in the muscles of both. This experiment may be extended, and contractions may thus be induced in a series of legs, the nerve of one being in contact with the muscles of another. This illustrates the great delicacy of the galvanoscopic frog's leg, as it will indicate a current due to a single muscular contraction, which does not affect an ordinary galvanometer. It is conclusively proved that the "induced contraction," as just described, is not due to an actual propagation of the galvanic current, but to a stimulus produced by the muscular contraction itself, by the fact that the same phenomena occur when the first muscular contraction is produced by mechanical or chemical excitation of the nerve.

Galvanic Current from the Exterior to the Cut Surface of a Nerve.—Before we study certain phenomena presented in nerves a portion of which is subjected to the action of a constant galvanic current, it is important to note the fact, discovered many years ago by Du Bois-Reymond, that there exists in the nerves, as in the muscles,[2] a galvanic current from the exterior to their cut surface.[3] This fact has been confirmed by all who have investigated the subject of electrophysiology. It has been roughly estimated by Matteucci that the nerve-current has from one-eighth to one-tenth the

[1] MATTEUCCI, *Leçons sur les phénomènes physiques des corps vivants*, Paris, 1847, p. 268.

[2] See vol. i., Movements, p. 476.

[3] DU BOIS-REYMOND, *Untersuchungen über thierische Elektricität*, Berlin, 1849, S. 251, *et seq.*

intensity of the muscular current.[1] The existence of the nerve-current has, as far as we know, no more physiological significance than the analogous fact observed in the muscular tissue. It is presented in nerves removed from the body, and has no relation to their functional activity, whether in normal action or excited by artificial stimulation.

Effects of a Constant Galvanic Current upon the Nervous Irritability.—Aside from the disorganizing effect upon the nerves of a powerful constant current, which is due solely to decomposition of their substance, a feeble current has been found to exert an important influence upon the nervous irritability, according to the direction in which the current is passed. The law in accordance with which this influence is exerted is stated by Matteucci as follows:

"A continued electric current passed through a mixed nerve, the crural or the lumbar, for example, modifies the excitability of the nerve in a very different manner, according to its direction. The excitability is enfeebled by the passage of the direct current, and, on the contrary, it is preserved and augmented, at least within certain limits, by the inverse current. The time necessary in order that the current shall produce this modification is proportionate to the degree of excitability of the nerve and in inverse ratio to the intensity of the current. After the breaking of the circuit, the modification of the nerve tends to cease at a period that is short in proportion as the excitability of the nerve is great and the intensity of the current is feeble. This proposition explains the difference in the electro-physiological effects of the continued current according to its direction, the well-known phenomenon of voltaic alternations, and the periods discovered and specially studied by Marianini and Nobili."[2]

This law has been carefully studied and formularized, as above, by Matteucci, but its discovery is attributed by physi-

[1] MATTEUCCI, *Cours d'électro-physiologie*, Paris, 1858, p. 122. [2] Ibid., p. 39

ological writers to Pfaff.[1] After a time, varying with the excitability of the nerve and the intensity of the current, the direct current will destroy the nervous irritability, but this may be restored by repose, or more quickly by the passage of an inverse current. If the inverse current be passed first for a few seconds, a contraction follows the breaking of the circuit; and this contraction, within certain limits, is more vigorous the longer the current is passed. At the same time, the prolonged passage of the inverse current increases the excitability of the nerve for any kind of stimulus. When the inverse current has been passed through the nerves for several hours, breaking of the circuit is followed by very violent contraction and a tetanic condition of the muscles, enduring for several seconds.

Electrotonus, Anelectrotonus, and Catelectrotonus.

Many years ago, Du Bois-Reymond discovered the curious and interesting fact, that when a constant galvanic current is passed through a portion of a freshly-prepared nerve, those parts of the nerve not included between the poles are brought into a peculiar condition. While in this state, the nerve will deflect the needle of a delicate galvanometer and its excitability is modified.[2] The deflection of the needle, in this instance, is not due to the normal nerve-current, for it occurs when the galvanometer is applied to the surface of the nerve only. It is due to an electric tension of the entire nerve, induced by the passage of a current through a portion of its extent. This condition is called electrotonus. The phenomena thus produced have been most elaborately studied by Pflüger, who further recognized a peculiar condition of that portion of the nerve near the anode, or positive pole, differing from the condition of the nerve near the cathode, or negative pole. Near the anode, the excitability of the nerve is dimin-

[1] Longet, *Traité de physiologie*, Paris, 1869, tome iii., p. 194.

[2] Du Bois-Reymond, *Untersuchungen über thierische Elektricität*, Berlin, 1849, Bd ii., S. 289, *et seq.*

ished, and this condition has been called anelectrotonus.[1] Near the cathode, the excitability is increased, and this condition has been called catelectrotonus.[2]

These varied phenomena have been the subject of extended investigation by electro-physiologists; and although they are not to be ranked among the physiological properties of the nerves, they have considerable pathological and therapeutic importance. It is well known, for example, that electricity is one of the most efficient agents at our command for the restoration of the functions of nerves affected with disease; and the constant current has, particularly of late, been extensively and successfully used as a therapeutic agent. The constant current, in restoring the normal condition of nerves, must influence, not only that portion included between the poles of the battery, but the entire nerve; and the electrotonic condition, with its modifications, explains how this result may be obtained. Undoubtedly the sensory nerves are affected as well as the motor, though we have as yet but little positive information upon this point. A knowledge of the fact that the constant current diminishes the excitability of the nerve near the anode (anelectrotonos) and increases it near the cathode (catelectrotonos) may become important in determining the direction of the current to be employed in different cases of disease.

In the present condition of the subject of electro-physiology, it will be unnecessary to do more than to indicate, as clearly and simply as possible, the laws of the phenomena attending the passage of a constant current through nerves, as far as they have been definitively ascertained. For a most lucid exposition of these laws, the physiological student cannot do better than to consult a lecture recently published by Dr. Rutherford, of Edinburgh.[3]

[1] PFLÜGER, *Untersuchungen über die Physiologie des Electrotonus*, Berlin, 1859, S. 277, *et seq.*

[2] *Op. cit.*, S. 186, *et seq.*

[3] RUTHERFORD, *Electrotonus.—Journal of Anatomy and Physiology*, Cambridge and London, 1868, vol. ii., p. 87, *et seq.*

The phenomena of electrotonus are very simple; and it is only when we attempt to construct a theory to account for these phenomena that the subject becomes obscure. Suppose, for example, that a nerve be exposed in a living animal, or in one just killed, and a galvanic current be applied from a Grove's battery, in which about twelve square inches of zinc are exposed to the action of a liquid containing one part of ordinary sulphuric acid to eight of water.[1] A delicate galvanometer applied to the nerve either above or below the poles will indicate a decided current, much more intense than the tranquil nerve-current between the exterior and the cut surface. This electrotonic condition exists so long as the galvanic current is continued; and, as has been shown by Matteucci in operating upon the higher animals—rabbits, dogs, fowls, and sheep—when the galvanic current has been sufficiently powerful and prolonged, the electrotonic condition persists for a certain time after the stimulus has ceased.[2] As we have seen that the muscular contraction following galvanic stimulation of a nerve is powerful in proportion to the extent of nerve included between the poles of the battery, so the electrotonic condition increases in intensity with the length of the nerve subjected to the constant current; provided, always, that the strength of the current be slightly increased to compensate the enfeebling action due to the resistance in the increased length of the circuit.[3]

We do not propose to discuss fully the various theories that have been advanced in explanation of the phenomena of electrotonus. Matteucci has made a series of interesting observations upon conductors formed of very fine wires, one of platinum and the other of amalgamated zinc, covered with cotton thread soaked in a neutral solution of sulphate of

[1] Rutherford, *loc. cit.*

[2] Matteucci, *Origine de l'électrotone des nerfs.—Revue des cours scientifiques*, Paris, 1867–'68, tome v., p. 279.

Morgan, *Electro-physiology and Therapeutics*, New York, 1868, p. 495.

zinc. The experiments were then arranged so as to operate first with the platinum wire and afterward with the zinc, by passing a galvanic current through a small portion of the conductor, in the same way as it is passed through a portion of a nerve. He found that in this way he could produce a strong electrotonic current in the platinum wire, even at a distance of more than three feet from the electrodes, while no such current was observed in the zinc. He remarks that in the platinum wire "secondary polarities" are produced very powerfully and rapidly, while these are not developed in the zinc.[1] From these experiments alone, it might seem that the phenomena of electrotonus, as described by Du Bois-Reymond and others, are to be explained entirely by the physical properties of the nerves as conductors of electricity; but various observations on the nerves under different conditions have conclusively proven the contrary. All observers are agreed that the electrotonic condition is marked in proportion to the excitability of the nerve, and is either entirely absent or extremely feeble in nerves that are dead, or have lost their irritability. If a strong ligature be applied to the extra-polar portion of the nerve, or if the nerve be divided and the cut ends brought in contact with each other, the electrotonic condition is either not observed or is very feeble. These facts show conclusively that the phenomena of electrotonus depend upon the physiological integrity of nerves. A dead nerve, or one that has been divided or strongly ligatured, may present these phenomena under the stimulation of a very powerful current (and then only to a slight degree), when the condition depends upon the purely physical properties of the nerve as a conductor; but there is no comparison between these phenomena and those observed in nerves that retain their physiological properties. Were it otherwise, how could the physiological properties of a diseased nerve be restored throughout its whole extent by a constant current passed through a restricted portion, when the exci-

[1] *Revue des cours scientifiques*, Paris, 1867–'68, tome v., p. 279.

tability of the nerve is only manifested at the closing or opening of the circuit?[1]

Anelectrotonus and Catelectrotonus.—It is interesting to note that when a portion of a nerve is subjected to a moderately powerful constant current, the conditions of the extra polar portions corresponding to the two poles of the battery are entirely different. Near the positive pole, or anode, the excitability of the nerve and the rate of nervous conduction are diminished. If, however, we have a galvanometer applied to this portion of the nerve, its electromotive power, measured by the deflection of the galvanometric needle, is increased. On the other hand, near the negative pole, or cathode, the excitability of the nerve is increased as well as the rate of nervous conduction; but the electromotive power is diminished. The above is laid down by Rutherford, as the law of electrotonus.[2] These facts, at least so far as they relate to the increase of the excitability of the nerve near the cathode and its diminution near the anode, are partially explained by Matteucci upon purely physical principles, depending upon the electrolytic action of the current, as is shown by the following experiment:

Two cups are filled, the one with a very feeble alkaline solution, and the other with an equally weak acid fluid. A number of galvanoscopic frogs' legs are then rapidly prepared, of which one-half the number is plunged in the alkaline and one-half in the acid fluid, for from thirty seconds to one or two minutes. The parts are then removed from the liquids, and are carefully washed and dried in bibulous paper. By touching the nerves with a strong solution of

[1] It is necessary to note, in this connection, that Matteucci (*loc. cit.*) found that the electrotonic condition in the platinum wire covered with moistened cotton was affected by a strong ligature in nearly the same way as a living nerve, when, of course, "the alteration consists principally in the solution of continuity thus produced in the moist covering of the metallic thread."

[2] RUTHERFORD, *Electrotonus.—Journal of Anatomy and Physiology*, Cambridge and London, 1868, vol. ii., p. 98.

common salt, which is a powerful excitant for the nervous irritability, the nerves that had been exposed to the alkaline solution produced more powerful and prompt contractions than those exposed to the acid. Now the electrolytic action of a constant current tends to the accumulation of hydrogen and an alkali near the cathode, and oxygen and an acid near the anode; and by this, Matteucci explains the increase of excitability in catelectrotonus and the diminished excitability in anelectrotonus.[1] As regards this question, we have only to say, as in the case of general electrotonus, that the conditions are susceptible of a partial explanation on purely physical grounds; but precisely how far the unexplained physiological properties of the nerves are involved, it is impossible to say.

Neutral Point.—The anelectrotonic condition, on the one hand, and the catelectrotonic condition at the other pole of the battery, are marked in extra-polar portions of the nerve, and are to be recognized as well in that portion through which the current is passing; but between the poles, is a point where these conditions meet, as it were, and where the excitability is unchanged. This has been called the neutral point. When the galvanic current is of moderate strength, this neutral point is about half-way between the poles. "When a weak current is used, the neutral point approaches the positive pole, while in a strong current, it approaches the negative pole. In other words, in a weak current the negative pole rules over a wider territory than the positive pole, whereas in a strong current the positive pole prevails."[2]

Negative Variation.—There remains one curious phenomenon, discovered by Du Bois-Reymond, which depends

[1] MATTEUCCI, *Phénomènes physico-chimiques des corps vivants.—Revue des cours scientifiques*, Paris, 1867–'68, tome v., p. 579.

[2] RUTHERFORD, *loc. cit.*, p. 92.

upon the action of a rapidly-interrupted current applied to an excitable nerve. If a galvanometer be applied to a living nerve so as to indicate by its deviation the normal, or tranquil nerve-current, a rapidly-interrupted current of electricity passed through a portion of the nerve, it is well known, produces a tetanic condition of the muscles. If we now watch the needle of the galvanometer, it will be observed to retrograde, and will finally return to zero, indicating that the proper nerve-current has been overcome. This will be observed to a slight degree under the influence of mechanical or chemical stimulation of the nerve, the proper nerve-current being diminished, but generally not abolished. This variation of the needle under the influence of the tetanic condition has been called negative variation.[1] We do not yet know that it has any important physiological or pathological significance.

[1] DU BOIS-REYMOND, *Untersuchungen über thierische Elektricität*, Berlin, 1849, Bd. ii., S. 425, *et seq.*

CHAPTER IV.

SPINAL NERVES—MOTOR NERVES OF THE EYEBALL.

Special nerves coming from the spinal cord—Cranial nerves—Anatomical classification—Physiological classification—Motor oculi communis (third nerve) —Physiological anatomy—Properties and functions—Influence upon certain muscles of the eyeball—Action of the inferior oblique muscle—Influence upon the movements of the iris—Patheticus, or trochlearis (fourth nerve)—Physiological anatomy—Properties and function—Action of the superior oblique muscle—Motor oculi externus, or abducens (sixth nerve) —Physiological anatomy—Properties and function.

Spinal Nerves.

WITH a thorough knowledge of the general properties of the nerves belonging to the cerebro-spinal system, the functions of most of the special nerves are apparent simply from their anatomical relations. This is especially true of the spinal nerves; which, in general terms, are distributed to the muscles of the trunk and extremities, the sphincters, and to the integument covering these parts, the posterior segment of the head, and a portion of the mucous membranes. It is evident, therefore, that an account of the exact function of each nervous branch would necessitate a full description, not only of the nerves, but of the muscles of the body, which is manifestly within the scope only of elaborate treatises on descriptive anatomy. It is sufficient to indicate, in this connection, that there are thirty-one pairs of spinal nerves; eight cervical, twelve dorsal, five lumbar, five sacral, and one coccygeal. Each nerve arises from the spinal cord by an anterior (motor) and a posterior (sensory)

root; the posterior roots being the larger, and having a ganglion. Immediately beyond the ganglion, the two roots unite into a single mixed nerve, which passes out of the spinal canal by the intervertebral foramen. The nerve thus constituted is endowed with both motor and sensory properties. It divides outside of the spinal canal into two branches, anterior and posterior, both containing motor and sensory filaments, which are distributed respectively to the anterior and posterior parts of the body. The anterior branches are the larger, and supply the limbs and all parts in front of the spinal column.

The anterior branches of the four upper cervical nerves form the cervical plexus, and the four inferior cervical nerves, with the first dorsal, form the brachial plexus. The anterior branches of the dorsal nerves, with the exception of the first, supply the walls of the chest and abdomen. These nerves go directly to their distribution, and do not first form a plexus, like most of the other spinal nerves. The anterior branches of the four upper lumbar nerves form the lumbar plexus. The anterior branch of the fifth lumbar nerve and a branch from the fourth unite with the anterior branch of the first sacral, forming the lumbo-sacral nerve, and enter into the sacral plexus. The three upper anterior sacral nerves with a branch from the fourth form the sacral plexus. The greatest portion of the fourth anterior sacral is distributed to the pelvic viscera and the muscles of the anus. The fifth anterior sacral and the coccygeal are distributed about the coccyx.

The posterior branches of the spinal nerves are very simple in their distribution. With one or two exceptions, which have no great physiological importance, these nerves pass backward from the main trunk, divide into two branches, external and internal, and their filaments of distribution go to the muscles and integument behind the spinal column.

It is further important to note, as we shall have occasion to do more particularly in connection with the great sym-

pathetic nerve, that all of the cerebro-spinal nerves anastomose with the sympathetic. This anatomical connection between the two systems of nerves has great physiological interest.

Cranial Nerves.

The nerves which pass out from the cranial cavity present certain differences in their arrangement and general properties from the ordinary spinal nerves. As we have seen, the spinal nerves are exceedingly simple, each one being formed by the union of a motor and a sensory root. The function of most of them follows as a matter of course when we understand their general properties and anatomical distribution. Many of the cranial nerves, however, are peculiar, either as regards their general properties or in their distribution to parts concerned in special functions. In some of these nerves, the most important facts concerning their distribution have only been ascertained by physiological experimentation, and their anatomy is inseparably connected with their physiology. It would be desirable, if it were possible, to classify these nerves with reference strictly to their properties and functions; but this can be done only to a certain extent, and we must adopt as a basis those divisions recognized in the best works on anatomy.

The two classifications of the cranial nerves adopted by most anatomists are the arrangement of Willis[1] and of Sömmering.[2] The first of these is the more common, and in it the nerves are numbered from before backward in the order in which they pass out of the skull, making nine pairs.[3]

[1] WILLIS, *Cerebri Anatome: cui accessit Nervorum Descriptio et Usus*, Londini, 1664, p. 145, *et seq.*

[2] SÖMMERING, *De Basi Encephali et Originibus Nervorum*, Goettingae, 1778, p. 69, *et seq.*

[3] Haller adopted the classification of Willis, and his example has been followed by nearly all of the later anatomical and physiological writers, but he discards the tenth pair, the suboccipital, or first cervical nerve, originally reckoned by Willis with the cranial nerves (HALLER, *Elementa Physiologiæ*, Lausannæ, 1762, tomus iv., p. 240.)

Anatomical Classification of the Cranial Nerves.

First Pair.—Olfactory; special nerve of smell.

Second Pair.—Optic; special nerve of sight.

Third Pair.—Motor oculi communis; motor nerve distributed to all of the muscles of the eyeball, except the external rectus and the superior oblique, to the iris, and the levator palpebræ.

Fourth Pair.—Patheticus, or trochlearis; a motor nerve sent to the superior oblique muscle of the eye.

Fifth Pair.—A small motor root (nerve of mastication) distributed to the muscles of mastication, and a large root (the trifacial), the nerve of general sensibility of the face.

Sixth Pair.—Motor oculi externus, or abducens; a motor nerve passing to the external rectus muscle of the eye.

Seventh Pair.—Portio mollis, or auditory, a special nerve of hearing; and the portio dura, or facial; a motor nerve distributed to the superficial muscles of the face.

Eighth Pair.—Glosso-pharyngeal; pneumogastric, or par vagum; spinal accessory. Three mixed nerves, with quite extensive distributions.

Ninth Pair.—Sublingual, or hypoglossal; a motor nerve distributed to the tongue.[1]

Physiological Classification.

(a.) *Nerves of Special Sense.*

Olfactory.

Optic.

Auditory.

Gustatory, comprising a part of the glosso-pharyngeal and a small filament from the facial to the lingual branch of the fifth.

[1] According to the classification of Sömmering, the arrangement is the same for the first, second, third, fourth, fifth, and sixth. The facial is called the seventh; the auditory, the eighth; the glosso-pharyngeal, the ninth; the pneumogastric, the tenth; the spinal accessory, the eleventh; and the sublingual, the twelfth.

(b.) *Nerves of Motion.*

Nerves of motion of the eyeball; comprising the motor oculi communis, the patheticus, and the motor oculi externus.

Nerve of mastication, or motor root of the fifth.

Facial, sometimes called the nerve of expression.

Spinal accessory.

Sublingual.

(c.) *Nerves of General Sensibility.*

Trifacial, or large root of the fifth.

A portion of the glosso-pharyngeal.

Pneumogastric.

In the above arrangement, the nerves are classified according to their properties at their roots. In their course, some of these nerves become mixed, and their branches are both motor and sensory, such as the pneumogastric and the inferior maxillary branch of the trifacial.

The nerves of special sense are but slightly, if at all, endowed with general sensibility; and, with the exception of the gustatory nerves, do not present a ganglion on their roots, in this, also, differing from the ordinary sensory nerves. They are capable, therefore, of conveying to the nerve-centres only certain peculiar impressions, such as odors, for the olfactory nerves; light, for the optic nerves; sound, for the auditory nerves. The proper transmission of these impressions, however, involves the action of accessory organs, more or less complex; and we will pass over the properties of these nerves until we come to treat in full of the special senses.

Motor Oculi Communis (Third Nerve).

The third cranial nerve is the most important of the motor nerves distributed to the muscles of the eyeball. Its physiology is readily understood in connection with its distribution, the only point at all obscure being its relations to

the movements of the iris, upon which the results of experiments are somewhat contradictory. As a preface to the study of the functions of this nerve, it is necessary to describe its anatomical relations.

Physiological Anatomy.—Like all of the cranial nerves, this has an apparent origin, where it separates from the encephalon, and a deep origin, which is the last point to which its fibres can be traced in the substance of the brain; but the origin has not the physiological importance attached to its ultimate distribution.

The apparent origin of the nerve is from the inner edge of the crus cerebri, directly in front of the pons Varolii, midway between the pons and the corpora albicantia. It presents here from eight to ten filaments, of nearly equal size, which soon unite into a single, rounded trunk.

The deep origin of the nerve has been studied by dissections of the encephalon fresh and hardened by different liquids. Vulpian, who has made a great number of very careful dissections of these nerves, has been able to follow the fibres from their apparent origin into the brain-substance as far as the median line.[1] From the groove by which they emerge from the encephalon, the fibres spread out in a fan-shape, the middle filaments passing inward, the anterior, inward and forward, and the posterior, inward and backward. As the result of his observations, Vulpian concludes that the middle filaments pass to the median line, and decussate with corresponding fibres from the opposite side. The anterior filaments pass forward and are lost in the optic thalamus. The posterior filaments pass backward, and decussate beneath the aqueduct of Sylvius. This apparent decussation of the fibres of origin of the third nerves is important in connection with the harmony of action of the muscles of the eyes and the iris upon the two sides.

[1] VULPIAN, *Essai sur l'origine de plusieurs paires des nerfs craniens*, *Thèse*, Paris, 1853, p. 10, *et seq.*

The distribution of the third nerve is very simple. As it passes into the orbit by the sphenoidal fissure, it divides into two branches. The superior, which is the smaller, passes to the superior rectus muscle of the eye, and certain of its filaments are continued to the levator palpebræ superioris. The inferior division breaks up into three branches. The internal branch passes to the internal rectus muscle; the inferior branch, to the inferior rectus; the external branch, the largest of the three, is distributed to the inferior oblique muscle, and, in its course, sends a short and thick filament to the lenticular, or ophthalmic ganglion of the sympathetic. It is this branch which is supposed, through the short ciliary nerves passing from the lenticular ganglion, to furnish the motor influence to the iris.

In its course, this nerve receives a few very delicate filaments from the cavernous plexus of the sympathetic and a branch also from the ophthalmic division of the trifacial.

Properties and Functions of the Motor Oculi Communis.—Irritation applied to the root of the third nerve in a living animal produces contraction of the muscles to which it is distributed, but no pain. If the irritation, however, be applied a little farther on, in the course of the nerve, there are evidences of sensibility, which is readily explained by its communications with the ophthalmic branch of the trifacial. At its root, therefore, this nerve is exclusively motor, and its functions are connected entirely with the action of muscles. These facts have been experimentally demonstrated by Longet[1] and by Chauveau.[2]

Most of the important facts bearing upon the functions of the motor oculi are clearly demonstrable by dividing the nerve in a living animal, and are illustrated by cases of its

[1] Longet, *Traité de physiologie*, Paris, 1869, tome iii., p. 554.

[2] Chauveau, *Recherches physiologiques sur l'origine apparente et sur l'origine réelle des nerfs moteurs craniens.—Journal de la physiologie*, Paris, 1862, tome v., p. 274.

paralysis in the human subject. Herbert Mayo was one of the first to experiment upon this nerve in animals living or just killed, but his observations were made chiefly with reference to the movements of the iris.[1] Bernard,[2] Longet,[3] and all others who have divided the nerve in living animals, are agreed with regard to the phenomena following its section, which depend upon paralysis of the voluntary muscles. These phenomena are as follows:

1. Falling of the upper eyelid, or blepharoptosis.

2. External strabismus, immobility of the eye, except outward, inability to rotate the eye on its antero-posterior axis in certain directions, with slight protrusion of the eyeball.

3. Dilatation of the pupil, with a certain amount of interference with the movements of the iris.

The falling of the upper eyelid is constantly observed after division of the nerve in living animals, and always follows its complete paralysis in the human subject. An animal in which the nerve has been divided cannot raise the lid, but can approximate the lids more closely, by a voluntary effort. In the human subject, the falling of the lid gives to the face a very peculiar and characteristic expression. The complete loss of power shows that the levator palpebræ superioris muscle depends upon the third nerve entirely for its motor filaments. In pathology, external strabismus is very frequently observed without falling of the lid, the filament distributed to the levator muscle not being affected.

[1] MAYO, *Anatomical and Physiological Commentaries*, Number ii., London, 1823, p. 5; and, *Outlines of Human Physiology*, London, 1827, p. 294.

[2] BERNARD, *Leçons sur la physiologie et la pathologie du système nerveux*, Paris, 1858, tome ii., p. 204, *et seq.*

Bernard gives the following directions for division of the third nerve in the rabbit: A small steel hook is introduced along the external wall of the orbit into the middle temporal fossa. With the hook the nerve is caught at the anterior extremity of the fold of the dura mater, which is attached to the sella turcica, and torn across. In this operation, there are generally evidences of pain from the ophthalmic branch of the fifth as it is touched by the instrument.

[3] *Loc. cit.*

The external strabismus and the immobility of the eyeball except in an outward direction are due to paralysis of the internal, superior, and inferior recti muscles, the external rectus acting without its antagonist; a condition which requires no further explanation. These points are well illustrated by the experiment of dividing the nerve in rabbits. If the head of the animal be turned inward, exposing the eye to a bright light, the globe will turn outward, by the action of the external rectus; but if the head be turned outward, the globe remains motionless.[1]

It is somewhat difficult to note the effects of paralysis of the inferior oblique muscle, which is also supplied by the third nerve. This muscle, acting from its origin at the inferior and internal part of the circumference of the base of the orbit to its attachment at the inferior and external part of the posterior hemisphere of the eyeball, gives to the globe a movement of rotation on an oblique, horizontal axis, downward and backward, directing the pupil upward and outward. When this muscle is paralyzed, the superior oblique, having no antagonist, rotates the globe upward and inward, directing the pupil downward and outward. The action of the oblique muscles is observed when we move the head alternately toward one shoulder and the other. In the human subject, when the inferior oblique muscle on one side is paralyzed, the eye cannot move in a direction opposite to the movements of the head, as it does upon the sound side, so as to keep the pupil fixed, and the patient has double vision.[2]

When all the muscles of the eyeball, except the external rectus and superior oblique, are paralyzed, as they are by section of the third nerve, the globe is slightly protruded, simply by the relaxation of most of its muscles. An opposite action is easily observed in a cat with the facial nerve divided, so that it cannot close the lids. When the cornea is touched,

[1] BERNARD, *loc. cit.*

[2] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 555.

all of the muscles, particularly the four recti, act to draw the globe into the orbit, which allows the lid to fall slightly, and projects the little membrane which serves as a third eyelid in these animals.

Observations with regard to the influence of the third nerve upon the movements of the iris have not been so satisfactory in their results as those relating to the muscles of the eyeball. It will be remembered that this nerve sends a filament to the ophthalmic ganglion of the sympathetic, and that from this ganglion, the short ciliary nerves take their origin and pass to the iris. The ganglia of the sympathetic system receive branches both from motor and sensory nerves belonging to the cerebro-spinal system, and the ophthalmic ganglion is no exception to this rule. While it is undoubtedly true that division of the third nerve affects the movements of the iris, it becomes a question whether this be a direct influence, or an influence exerted primarily upon the ganglion, not, perhaps, differing from the general effects upon the sympathetic ganglia that follow destruction of their branches of communication with the motor nerves. As yet we know little of the reciprocal influences of the cerebro-spinal and the sympathetic system; but some of the researches of Bernard into the influence of the sympathetic ganglia upon the salivary secretion show that the submaxillary ganglion, at least, becomes paralyzed, or loses its influence over the secretion of the submaxillary gland, after it has been separated for a certain time from the cerebro-spinal system.[1] These considerations, however, belong more properly to the sympathetic system.

The most important experimental observations with regard to the influence of the third nerve on the iris are the following: Herbert Mayo made experiments on thirty pigeons, living or just killed, upon the action of the optic, the third, and the fifth nerves on the iris. He states that when the

[1] BERNARD, *Recherches expérimentales sur les nerfs vasculaires et calorifiques.—Journal de la physiologie*, Paris, 1862, tome v., p. 409.

third nerves are divided in the cranial cavity in a living pigeon, the pupils become fully dilated, and do not contract on the admission of intense light; and, when the same nerves are pinched in the living or dead bird, the pupils are contracted for an instant on each injury of the nerves. The same results follow division or irritation of the optic nerves under similar conditions; but when the third nerves have been divided, no change in the pupil ensues on irritating the entire or divided optic nerves.[1]

The above experiments are accepted by nearly all physiological writers; and the assumption is that the third nerves animate the muscular fibres that contract the pupil, the contraction produced by irritation of the optic nerves being reflex in its character. Later observers, however, have carried their experiments somewhat further. Longet divided the motor oculi and the optic nerve upon the right side. He found that irritation of the central end of the divided optic nerve produced no movement of the pupil of the side upon which the motor oculi had been divided, but caused contraction of the iris upon the other side. This, taken in connection with the fact that, in amaurosis affecting one eye, the iris on the affected side will not contract under the stimulus of light applied to the same eye, but will act when the uninjured eye is exposed to the light, further illustrates the reflex action which takes place through these nerves.[2]

The reflex action by which the iris is contracted is not instantaneous, like most of the analogous phenomena observed in the cerebro-spinal system, and its operations are rather characteristic of the sympathetic system and the non-striated muscular tissue. It has been found, also, by Bernard, in experiments upon rabbits, that the pupil is not immediately dilated after division of the third nerve. The method employed by Bernard, introducing a hook into the

[1] MAYO, *Anatomical and Physiological Commentaries*, Number ii., London, 1823, p. 4.

[2] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 556.

middle temporal fossa through the orbit and tearing the nerve, can hardly be accomplished without touching the ophthalmic branch of the fifth, which produces intense pain, and is always followed by a more or less persistent contraction of the pupil. Several hours after the operation, however, the pupil is generally found dilated, and may slowly contract when the eye is exposed to the light. In one experiment, this occurred after the eye had been exposed for an hour. But further experiments by Bernard show that although the pupil contracts feebly and slowly under the stimulus of light after division of the motor oculi, it will dilate under the influence of belladonna, and can be made to contract by operating upon other nerves. It is well known, for example, that division or irritation of the fifth nerve produces contraction of the pupil. This takes place after division of the third nerve as well as before. Section of the sympathetic in the cervical region also contracts the pupil, and this occurs after paralysis of the motor oculi.[1] These facts show that the third nerve is not the only one capable of acting upon the iris, and that it is not the sole avenue for the transmission of reflex influences.

Bernard also found that galvanization of the motor oculi itself did not produce contraction of the pupil, but this result followed when he galvanized the ciliary nerves coming from the ophthalmic ganglion.[2] Chauveau states, that in experiments upon horses, he has not observed contraction of the pupil following galvanization of the motor oculi, though he has sometimes seen it in rabbits.[3] At all events, contraction is by no means constant; and when it occurs, it probably depends upon stimulation of the ciliary nerves themselves or irritation of the ophthalmic branch of the fifth, and not upon stimulation of the trunks of the third pair.

[1] BERNARD, *Système nerveux*, Paris, 1858, tome ii., p. 201, *et seq.*

[2] *Op cit.*, p. 211.

[3] CHAUVEAU, *Recherches physiologiques sur l'origine apparante et sur l'origine réelle des nerfs moteurs craniens.—Journal de la physiologie*, Paris, 1862, tome v., p. 274.

The movements of the iris will be treated of again, in connection with the physiology of vision; but we may here allude to an interesting fact observed by Müller, which relates to the action of the motores oculorum. When the eye is turned inward by a voluntary effort, the pupil is always contracted; and when the axes of the two eyes are made to converge strongly, as in looking at near objects, the contraction is very great.[1]

The following case, kindly sent for examination by Dr. Althof, of the New York Eye Infirmary, illustrates, in the human subject, nearly all of the phenomena following paralysis of the motor oculi communis in experiments upon the lower animals:

The patient was a girl, nineteen years of age, with complete paralysis of the nerve upon the left side. There was slight protrusion of the eyeball, complete ptosis, with the pupil moderately dilated and insensible to ordinary impressions of light. The sight was not affected, but there was double vision, except when objects were placed before the eyes so that the axes were parallel, or when an object was seen with but one eye. The axis of the left eye was turned outward, but it was not possible to detect any deviation upward or downward. Upon causing the patient to incline the head alternately to one shoulder and the other, it was evident that the affected eye did not rotate in the orbit but moved with the head. This seemed to be a case of complete and uncomplicated paralysis of the third nerve

Patheticus, or Trochlearis (Fourth Nerve).

Except as regards the influence of the motor oculi communis upon the iris, the patheticus is to be classed with the other motor nerves of the eyeball. Its physiology is extremely simple, and resolves itself into the action of a single muscle, the superior oblique. It will be necessary, therefore, only to describe its origin, distribution, and connections.

[1] MÜLLER, *Elements of Physiology*, London, 1840, vol. i., p. 827.

Physiological Anatomy.—The apparent origin of the patheticus is from the superior peduncles of the cerebellum; but it may be easily traced to the valve of Vieussens. According to Vulpian, the deep roots, which are covered by an extremely thin layer of nerve-substance, can be traced, passing from without inward, to the following parts: One filament is lost in the substance of the peduncles; other filaments pass from before backward into the valve of Vieussens and are lost, and a few pass into the frenulum; a few filaments pass backward and are lost in the corpora quadrigemina; but the greatest number pass to the median line and decussate with corresponding filaments from the opposite side. Vulpian states that this decussation is quite as distinct as that of the anterior pyramids of the medulla oblongata, and that he has been able to follow fibres across the median line on either side.[1] The decussation of the fibres of origin of the fourth nerves has the same physiological significance as the decussation of the roots of the third.

From this origin, the patheticus passes into the orbit by the sphenoidal fissure, and is distributed to the superior oblique muscle of the eyeball. In the cavernous sinus, it receives branches of communication from the ophthalmic branch of the fifth, but these are not closely united with the nerve. A small branch passes into the tentorium, and one joins the lachrymal nerve, these, however, being exclusively sensitive and coming from the ophthalmic branch of the fifth.[2] It also receives a few filaments from the sympathetic.

Properties and Functions of the Patheticus.—Direct observations upon the patheticus in living animals have shown that it is motor, and its galvanization excites contraction of the superior oblique muscle only. These facts have been

[1] Vulpian, *Essai sur l'origine de plusieurs paires des nerfs craniens, Thèse,* Paris, 1853, p. 15.

[2] Sappey, *Traité d'anatomie descriptive*, Paris, 1852, tome ii., p. 209.

ascertained by Longet[1] and by Chauveau.[2] The question of the function of the nerve, therefore, resolves itself simply into the mode of action of the superior oblique muscle. This muscle arises just above the inner margin of the optic foramen, passes forward, along the upper wall of the orbit at its inner angle, to a little cartilaginous ring which serves as a pulley. From its origin to this point it is muscular. Its tendon becomes rounded just before it passes through the pulley, where it makes a sharp curve, passes outward and slightly backward, and becomes spread out to be attached to the globe at the superior and external part of its posterior hemisphere. It acts upon the eyeball from the pulley at the upper and inner portion of the orbit as the fixed point, and rotates the eye upon an oblique, horizontal axis, from below upward, from without inward, and from behind forward. By its action, the pupil is directed downward and outward. It is the direct antagonist of the inferior oblique, the action of which has been described in connection with the motor oculi communis. When the patheticus is paralyzed, the eyeball is immovable, as far as rotation is concerned; and when the head is moved toward the shoulder, the eye does not rotate to maintain the globe in the same relative position, and we have double vision.[3]

Motor Oculi Externus, or Abducens (*Sixth Nerve*).

Like the patheticus, the motor oculi externus is distributed to but a single muscle, the external rectus. Its uses, therefore, are apparent from a study of its properties and distribution.

Physiological Anatomy.—The apparent origin of the sixth nerve is from the groove which separates the anterior

[1] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 559.

[2] CHAUVEAU, *Recherches physiologiques sur l'origine apparante et sur l'origine réelle des nerfs moteurs craniens.—Journal de la physiologie*, Paris, 1862, tome v., p. 275.

[3] See page 130.

corpus pyramidale of the medulla oblongata from the pons Varolii, and from the upper portion of the medulla and the lower portion of the pons next the groove. Its origin at this point is by two roots: an inferior, which is the larger, and comes from the corpus pyramidale; and a superior root, sometimes wanting, which seems to come from the lower portion of the pons. All anatomists are agreed that the deep fibres of origin of this nerve pass to the gray matter in the floor of the fourth ventricle. Vulpian has followed these fibres to within about two-fifths of an inch of the median line, but could not trace them beyond this point.[1] It is not known that the fibres on the two sides decussate.

From this origin, the nerve passes into the orbit by the sphenoidal fissure, and is distributed exclusively to the external rectus muscle of the eyeball. In the cavernous sinus, it anastomoses with the sympathetic through the carotid plexus and Meckel's ganglion. It also receives sensitive filaments from the ophthalmic branch of the fifth. It is stated by Longet,[2] Sappey,[3] and others, that this nerve occasionally sends a small filament to the ophthalmic ganglion; and it is supposed by Longet that this branch, which is exceptional, exists in those cases in which paralysis of the motor oculi communis, which usually furnishes all the motor filaments to this ganglion, is not attended with immobility of the iris.

Properties and Functions of the Motor Oculi Externus.—Direct experiments, the most satisfactory being those of Longet[4] and of Chauveau,[5] have shown that the motor oculi communis is entirely insensible at its origin, its stimulation producing contraction of the external rectus muscle and no

[1] Vulpian, *Essai sur l'origine de plusieurs paires des nerfs rachidiens*, *Thèse*, Paris, 1853, p. 29.

[2] Longet, *Traité de physiologie*, Paris, 1869, tome iii., p. 561.

[3] Sappey, *Traité d'anatomie descriptive*, Paris, 1852, tome ii., p. 249.

[4] Longet, *op. cit.*, tome iii., p. 560.

[5] Chauveau, *op. cit.*—*Journal de la physiologie*, Paris, 1862, tome v., p. 275.

pain. The same experiments illustrate the function of the nerve, inasmuch as its irritation is followed by powerful contraction of the muscle and deviation of the eye outward. Division of the nerve in the lower animals or its paralysis in the human subject is attended with internal, or converging strabismus, from the unopposed action of the internal rectus muscle.

With regard to the associated movements of the eyeball, it is a curious fact that all of the muscles of the eye that have a tendency to direct the pupil inward or to produce the simple movements upward and downward; viz., the internal, inferior, and superior recti, are animated by a single nerve, the motor oculi communis, this nerve also supplying the inferior oblique; and that each muscle that has a tendency to move the globe so as to direct the pupil outward, except the inferior oblique; viz., the superior oblique and the external rectus, is supplied by a special nerve. The various movements of the eyeball will be studied more minutely in connection with the physiology of vision.

CHAPTER V.

MOTOR NERVES OF THE FACE.

Nerve of mastication (the small, or motor root of the fifth)—Physiological anatomy—Deep origin—Distribution—Properties and functions of the nerve of mastication—Facial nerve, or nerve of expression (the portio dura of the seventh)—Physiological anatomy—Intermediary nerve of Wrisberg—Decussation of the fibres of origin of the facial—Alternate paralysis—Course and distribution of the facial—Anastomoses with sensitive nerves—Summary of the anastomoses and distribution of the facial—Properties and functions of the facial—Functions of the branches of the facial within the aqueduct of Fallopius—Functions of the chorda tympani—Influence of various branches of the facial upon the movements of the palate and uvula—Functions of the external branches of the facial.

The motor nerves of the face are, the small, or motor root of the fifth, and the portio dura of the seventh, or the facial. The first of these nerves is distributed to the deep muscles, those concerned in the act of mastication, and the second, the facial, supplies the superficial muscles of the face, and is sometimes called the nerve of expression. These nerves are not so simple in their anatomy and physiology as the motor nerves of the eyeball. The nerve of mastication, at its origin, is deeply situated at the base of the brain, and is exposed and operated upon with difficulty. It passes out of the cranium, closely united with one of the great sensitive branches of the fifth, and its distribution has been most successfully studied by experiments in which it is divided in the cranial cavity. The origin of the facial is also reached with great difficulty. It communicates with other nerves, and its physiology has been most satisfactorily studied by di-

viding it at its origin or in different portions of its course. In treating of these nerves, we shall first, as in the case of the motor nerves of the eye, study their properties at their roots, noting the phenomena following their galvanization and section. It will be necessary, also, to describe their origin and distribution, as far as has been ascertained by dissection.

Nerve of Mastication (the Small, or Motor Root of the Fifth).

The motor root of the fifth nerve is entirely distinct from its sensitive portion, until it emerges from the cranial cavity by the foramen ovale. It is then closely united with the inferior maxillary branch of the large root; but at its origin it has been shown to be motor, and its section in the cranial cavity has demonstrated its distribution to a particular set of muscles.

Physiological Anatomy.—The apparent origin of the fifth nerve is from the lateral portion of the pons Varolii. The small, or motor root arises from a point a little higher and nearer the median line than the large root, from which it is separated by a few fibres of the white substance of the pons. The most satisfactory investigations with regard to the deep origin of the small root are those of Vulpian. According to this observer, the dissections should be made after the specimen has been kept in alcohol for about fifteen days, and before the parts are thoroughly hardened. At the point of apparent origin, the small root presents from six to eight rounded filaments. If a thin layer of the pons covering these filaments be removed, the roots will be found penetrating its substance, becoming flattened, passing under the superior peduncles of the cerebellum, and going to the anterior wall of the fourth ventricle. At this point, they change their direction, passing now from without inward, and from behind forward toward the median line, the fibres diverging

rapidly. The posterior fibres pass to the median line, and Vulpian has seen certain of these decussate with fibres from the opposite side. The anterior fibres pass toward the aqueduct of Sylvius and are lost. The fibres become changed in their character when they are followed inward beyond the anterior wall of the fourth ventricle. Here they lose their white color, become gray, and present numerous globules of gray substance between their filaments.[1]

From the origin above described, the small root passes beneath the ganglion of Gasser, from which it sometimes, though not constantly, receives a filament of communication, lies behind the inferior maxillary branch of the large root, and passes out of the cranial cavity by the foramen ovale. Within the cranium, the two roots are distinct; but after the small root passes through the foramen, it is united by a mutual interlacement of fibres with the sensitive branch.[2]

The course of the motor root of the fifth possesses little physiological interest. It is sufficient in this connection to note that the inferior maxillary nerve, made up of the motor root and the inferior maxillary branch of the sensitive root, just after it passes out by the foramen ovale, divides into two branches, anterior and posterior. The anterior branch, which is the smaller, is composed almost entirely of motor filaments, and is distributed to the muscles of mastication. It gives off five branches. The first of these passes to be distributed to the masseter muscle, in its course occasionally giving off a small branch to the temporal muscle and a filament to the articulation of the inferior maxillary with the temporal bone. The two deep temporal branches are distributed to the temporal muscle. The buccal branch sends filaments to the external pterygoid and to the temporal muscle, and a small branch is distributed to the internal pterygoid muscle. From the posterior branch, which

[1] VULPIAN, *Essai sur l'origine de plusieurs paires des nerfs craniens, Thèse*, Paris, 1853, p. 21.

[2] SAPPEY, *Traité d'anatomie descriptive*, Paris, 1852, tome ii., p. 233.

is chiefly sensitive, but contains some motor filaments, branches are sent to the mylo-hyoid muscle, and to the anterior belly of the digastric. In addition, the motor branch of the fifth sends filaments to the tensor muscles of the velum palati.

The above description shows, in general terms, the distribution of the nerve of mastication, without taking into consideration its various anastomoses, the most important of which are with the facial. Physiological experiments have shown that the buccinator muscle receives no motor filaments from the fifth, but is supplied entirely by the facial. Mayo found that pinching the branch of the fifth which penetrates the buccinator muscle produced no action upon it.[1] Longet has galvanized the buccal branch of the fifth without producing contraction of this muscle, which always contracts upon galvanizing the facial.[2] The buccal branch of the fifth sends motor filaments only, to the external pterygoid and the temporal, its final branches of distribution being sensitive and going to integument and mucous membrane.

In another volume we have given a table of the muscles of mastication, with a description of their action.[3] It will be seen by this table that the following muscles depress the lower jaw; viz., the anterior belly of the digastric, the mylo-hyoid, the genio-hyoid, and the platysma myoides. Of these, the digastric and the mylo-hyoid are animated by the motor root of the fifth; the genio-hyoid is supplied by filaments from the sublingual; and the platysma myoides, by branches from the facial and from the cervical plexus. All of the muscles which elevate the lower jaw and move it laterally and antero-posteriorly; viz., the temporal, masseter, and the internal and external pterygoids, the muscles most

[1] Mayo, *Anatomical and Physiological Commentaries*, Number ii., London, 1823, p. 8.

[2] Longet, *Traité de physiologie*, Paris, 1869, tome iii., p. 563.

[3] See vol. ii., Digestion, p. 147, *et seq.*

actively concerned in mastication, are animated by the motor root of the fifth.

Properties and Functions of the Nerve of Mastication.—The anatomical distribution of the small root of the fifth nerve points at once to its function. Charles Bell, whose ideas of the nerves were derived almost entirely from their anatomy, called it the nerve of mastication, in 1821, though he does not state that any experiments were made with regard to its function.[1] All anatomical and physiological writers since that time have adopted this view. It would be difficult, if not impossible, to galvanize the root in the cranial cavity in a living animal; but its galvanization, probably in an animal just killed, has been shown by Longet, before 1842, to determine very marked movements of the lower jaw.[2] Longet states in his work on physiology that no contractions of the muscles of mastication are produced when the large root of the fifth alone is galvanized. The experiments demonstrating this fact were made on horses and dogs, operating upon the roots of the nerves after removing the cerebral lobes.[3] Chauveau also found that galvanization of the small root of the fifth produced contraction of the muscles which elevate the lower jaw sufficiently sudden and violent to break sometimes, in old horses, little fragments from the irregular surfaces of the teeth.[4]

The above experiments are sufficient to show the physiological properties of the small root, which is without doubt solely a nerve of motion.

[1] BELL, *On the Nerves; giving an Account of some Experiments on their Structure and Functions, which lead to a New Arrangement of the System.—Philosophical Transactions*, London, 1821, Part i., p. 417.

[2] LONGET, *Anatomie et physiologie du système nerveux*, Paris, 1842, tome ii., p. 190.

[3] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 562.

[4] CHAUVEAU, *Recherches physiologiques sur l'origine apparante et sur l'origine réelle des nerfs moteurs craniens.—Journal de la physiologie*, Paris, 1862, tome v., p. 276.

The observations upon the division of the fifth pair in the cranial cavity, made by Fodéra, Mayo, Magendie, Bernard, and others, are most interesting in connection with the functions of its sensitive branches, and will be referred to in detail in treating of the properties of the large root. In addition to the loss of sensibility following section of the entire nerve, Bernard has noted carefully the effects of division of the small root, which cannot be avoided in the operation. In rabbits, the paralysis of the muscles of mastication upon one side, and the consequent action of the muscles upon the unaffected side only, produce, a few days after the operation, a remarkable change in the appearance of the incisor teeth. As the teeth in these animals are gradually worn away in mastication and reproduced, the lower jaw being deviated by the action of the muscles of the sound side, the upper incisor of one side and the lower incisor of the other touch each other but slightly and the teeth are worn unevenly. This makes the line of contact between the four incisors, when the jaws are closed, oblique instead of horizontal.[1] We have often divided the fifth pair in the cranial cavity in rabbits, by the method employed by Magendie and Bernard, and have repeatedly verified these observations.

There is little left to say with regard to the functions of the motor root of the fifth nerve, in addition to our description of the action of the muscles of mastication, contained in the volume on digestion,[2] except as regards the action of the filaments sent to the muscles of the velum palati. In deglutition, the muscles of mastication are indirectly involved. This act cannot be well performed unless the mouth be closed by these muscles. When the food is brought in contact with the velum palati, muscles are brought into action which render this membrane tense, so that the opening is adapted to the size of the alimentary bolus. These muscles

[1] Bernard, *Leçons sur la physiologie et la pathologie du système nerveux*, Paris, 1858, tome ii., p. 100.

[2] See vol. ii., Digestion, p. 147, *et seq.*

are animated by the motor root of the fifth. This nerve, then, is not only the nerve of mastication, animating all of the muscles concerned in this act, except two of the most unimportant depressors of the lower jaw (the genio-hyoid and the platysma myoides), but it is concerned indirectly in deglutition.

Facial Nerve, or Nerve of Expression (*the Portio dura of the Seventh*).

The facial, the portio dura of the seventh according to the arrangement of Willis, is one of the most interesting of the cranial nerves. Its anatomical relations are quite intricate, and its communications with other nerves, very numerous. As far as can be determined by experiments upon living animals, this nerve is exclusively motor at its origin; but in its course it presents anastomoses with the sympathetic, with branches of the fifth, and with the cervical nerves, undoubtedly receiving sensory filaments. While the chief physiological interest attached to this nerve depends upon its action upon muscles, it is important to study its origin, distribution, and communications.

Physiological Anatomy.—The portio dura of the seventh has its apparent origin from the lateral portion of the medulla oblongata, in the groove between the olivary and the restiform body, just below the border of the pons Varolii, its trunk being internal to the trunk of the portio mollis, or auditory nerve. It is separated from the auditory by the two filaments constituting what is known as the intermediary nerve of Wrisberg, or the *portio inter duram et mollem.* As this little nerve joins the facial, it must be included in its root. It is called the accessory root by Sappey.[1]

There are certain pathological considerations which render the deep, or real origin of the facial a question of the

[1] SAPPEY, *Traité d'anatomie descriptive*, Paris, 1852, tome ii., p. 251.

greatest interest and importance. In hemiplegia from injury of the substance of the encephalon, particularly from hæmorrhage, there is almost always more or less paralysis of the superficial muscles of the face. It has been observed that in certain cases, the facial paralysis exists upon the same side as the hemiplegia, the side opposite to the cerebral lesion, while in others, the palsy of the face is on the same side as the lesion, the general hemiplegia being, as usual, upon the opposite side. To explain these phenomena theoretically, we must assume that in some cases, the brain-lesion is to be located at a point where it involves the filaments of origin of the facial, following them from without inward, before they decussate, which would produce facial paralysis on the same side as the lesion and none on the side affected with general hemiplegia; while in other cases, the injury to the brain involves the roots of the facial after they have decussated, when the paralysis of the face would be on the same side as the paralysis of the rest of the body. It would be interesting to see how far these pathological facts, with their theoretical explanation, correspond with anatomical researches into the real origin of the nerves.

Many anatomists have endeavored to trace the fibres of the facial from their point of emergence from the encephalon to their true origin, but with results not entirely satisfactory. At the present day, it is pretty generally agreed that the fibres pass inward, with one or two deviations from a straight course, to the floor of the fourth ventricle, where they spread out and become fan-shaped. In the floor of the fourth ventricle, certain of the fibres have been thought to terminate in the cells of the gray substance, and others have been traced to the median line, where they decussate; the course of most of the fibres, however, has never been satisfactorily established.

It is evident, from physiological experiments, that the decussation of the fibres in the floor of the fourth ventricle itself is not very important. Vulpian has made, in dogs

and rabbits, a longitudinal section in the middle line of the ventricle, which would necessarily have divided the fibres passing from one side to the other, without producing notable paralysis of the facial nerves upon either side.[1] This single fact is sufficient to show that the main decussation of the fibres animating the muscles of the face takes place, if at all, at some other point.

The following curious phenomenon, however, resulting from this section, was noted by Vulpian: He found that although there was no apparent paralysis of the orbicularis muscle of the eye upon either side, the synchronism of the movements of the two muscles seemed to be destroyed. It is well known that in man, and in many of the lower animals, there is an involuntary action of these muscles simultaneously on the two sides in winking. After a longitudinal section in the median line of the floor of the fourth ventricle, the animals winked with either eye alternately, or with one eye for a time without closing the other, but there was no simultaneous action of the muscles on the two sides.[2]

The pathological facts bearing upon the question of decussation of the filaments of origin of the facial have long been recognized. They are, in brief, as follows: When there is a lesion of the brain-substance anterior to the pons Varolii, the phenomena due to paralysis of the facial are observed on the same side as the hemiplegia, opposite to the side of injury to the brain. When the lesion is either in the pons or below it, the face is affected on the same side, and not on the side of the hemiplegia. In view of these facts, the remarkable phenomenon of hemiplegia upon one side and facial paralysis upon the other is regarded as indicating, with tolerable certainty, that the injury to the brain has occurred upon the same side as the facial paralysis, either in or posterior to the pons Varolii. It is unnecessary

[1] Vulpian, *Leçons sur la physiologie générale et comparée du système nerveux*, Paris, 1866, p. 480.

[2] Vulpian, *op. cit.*, p. 481.

to enter into a farther discussion of these facts, which are accepted by nearly all writers upon diseases of the nervous system, and may be regarded as settled;[1] and the only question is, how far they can be explained by the anatomy of the parts.

As we have just seen, the fibres of origin of the facial have been traced to the floor of the fourth ventricle, where a few decussate, but the rest are lost. The question now is, whether or not the fibres pass up through the pons, and decussate above, as the pathological facts just noted would seem to indicate. Anatomical researches upon this point are entirely unsatisfactory; and the existence of such a decussation has never been clearly demonstrated. The pathological observations, nevertheless, remain; and, however indefinite anatomical researches may have been, there can be no doubt that lesions in one-half of the pons affect the facial upon the same side, while lesions above have a crossed action. The most that we can say upon this point is, that it is a reasonable inference from pathological facts that the nerves decussate anterior to the pons.

It will be only necessary to describe in a general way the course of the fibres of distribution of the facial. The main root of the facial, the auditory nerve, and the delicate intermediary nerve of Wrisberg pass together into the internal auditory meatus. At the bottom of the meatus, the facial and the nerve of Wrisberg enter the aquæductus Fallopii, following its course through the petrous portion of the temporal bone. In the aqueduct, the nerve of Wrisberg presents a little ganglioform enlargement, of a reddish color, which has been shown to contain nerve-cells.[2] The main

[1] The reader is referred for a fuller consideration of these points to the recent standard works upon practical medicine. The most complete collection of cases of the so-called alternate paralysis was published by Gubler, in the *Gazette hebdomadaire de médecine et chirurgie*, Paris, 1856, and in the volumes of the same journal for 1858 and 1859. A characteristic case has lately been reported by Prof. Hammond, in the *Journal of Psychological Medicine*, New York, 1871, vol. v., p. 14.

[2] Sappey, *Traité d'anatomie descriptive*, Paris, 1862, tome ii., p. 254.

root and the intermediary nerve then unite and form the common trunk of the facial, which emerges from the cranial cavity by the stylo-mastoid foramen.

In the aquæductus Fallopii, the facial gives off numerous branches, as follows:

1. The large petrosal branch is given off from the ganglioform enlargement, and goes to Meckel's ganglion.

2. The small petrosal branch is given off at the ganglioform enlargement, or a very short distance beyond it, and passes to the otic ganglion.

3. A small branch, the tympanic, is distributed to the stapedius muscle.

4. The chorda tympani, a branch of great physiological interest, passes through the cavity of the tympanum, and joins the lingual branch of the inferior maxillary division of the fifth as it passes between the two pterygoid muscles, with which nerve it becomes closely united.

5. Opposite to the point of origin of the chorda tympani, a communicating branch passes between the facial and the pneumogastric, connecting these nerves by a double inosculation.

The five branches above described are given off in the aquæductus Fallopii.[1] The following branches are given off after the nerve has emerged from the cranial cavity:

1. Just after the facial has passed out at the stylo-mastoid foramen, it sends a small communicating branch to the glosso-pharyngeal nerve. According to Sappey, this branch is sometimes wanting.[2]

2. The posterior auricular nerve is given off by the facial a little below the stylo-mastoid foramen. Its superior branch is distributed to the retrahens aurem and the attollens aurem.

[1] In the course of the facial in the aqueduct, two branches are sometimes described, one going to the auditory, and another to the sympathetic filaments accompanying the middle meningeal artery; but their existence is denied by many anatomists.

[2] SAPPEY, *Traité d'anatomie descriptive*, Paris, 1852, tome ii., p. 259.

In its course, this nerve receives a communicating branch of considerable size from the cervical plexus, by the auricularis magnus. It sends some filaments to the integument. The inferior, or occipital branch, the larger of the two, is distributed to the occipital portion of the occipito-frontalis muscle and to the integument.

3. The digastric branch is given off near the root of the posterior auricular. It is distributed to the posterior belly of the digastric muscle. In its course, it anastomoses with filaments from the glosso-pharyngeal nerve. From the plexus formed by this anastomosis, filaments are given off to the digastric and to the stylo-hyoid muscle.

4. Near the stylo-mastoid foramen, a small branch is given off, which is distributed exclusively to the stylo-hyoid muscle.

5. Near the stylo-mastoid foramen, or sometimes a little above it, a long and exceedingly delicate branch is given off, which is not noticed in most works on anatomy. It is described, however, by Hirschfeld, under the name of the lingual branch.[1] It passes behind the stylo-pharyngeal muscle, and then by the sides of the pharynx to the base of the tongue. In its course, it receives one or two branches from the glosso-pharyngeal nerve, which are nearly as large as the original branch from the facial. As it passes to the base of the tongue, it anastomoses again by numerous filaments with the glosso-pharyngeal. It then sends filaments of distribution to the mucous membrane, and finally passes to the stylo-glossus and the palato-glossus muscle.

Having given off these branches, the trunk of the facial passes through the parotid gland, dividing into its two great terminal branches.

1. The temporo-facial branch, the larger, passes upward and forward to be distributed to the superficial muscles of the upper part of the face; viz., the attrahens aurem, the

[1] Ludovic Hirschfeld, *Traité et iconographie du système nerveux*, Paris, 1866, p. 206, and, *Atlas*, Pl. xxx., Figs. 2, 13.

frontal portion of the occipito-frontalis, the orbicularis palpebrarum, corrugator supercilii, pyramidalis nasi, levator labii superioris, levator labii superioris alæque nasi, the dilators and compressors of the nose, part of the buccinator, the levator anguli oris, and the zygomatic muscles. In its course, it receives branches of communication from the auriculo-temporal branch of the inferior maxillary nerve. It joins also with the temporal branch of the superior maxillary and with branches of the ophthalmic. In its course, it thus becomes a mixed nerve, and is distributed in part to integument.

2. The cervico-facial nerve passes downward and forward to supply the buccinator, orbicularis oris, risorius, levator labii inferioris, depressor labii inferioris, depressor anguli oris, and platysma.

Summary of the Anastomoses and Distribution of the Facial.—In the aquæductus Fallopii, filaments of communication go to Meckel's ganglion and the otic ganglion of the sympathetic. The chorda tympani joins the lingual branch of the inferior maxillary division of the fifth. A branch is also sent to the pneumogastric. After the nerve has passed out by the stylo-mastoid foramen, it sends a communicating branch to the glosso-pharyngeal, and receives a branch from the auricularis magnus. It anastomoses, also, outside of the cranium, with the glosso-pharyngeal. In the course of the nerve, it receives anastomosing filaments from the three great divisions of the fifth.

It is thus seen that the facial, in its course, receives numerous filaments from the great sensitive nerve of the face. Certain of its fibres of distribution go to integument.

The muscles supplied by the facial are the stapedius, and probably the tensor tympani, of the internal ear, the muscles of the external ear, the occipito-frontalis, the posterior belly of the digastric, the stylo-hyoid, the stylo-glossus, and the palato-glossus. The two great branches of distribution, the temporo-facial and the cervico-facial, are distributed to all of

the superficial muscles of the face, leaving the deep muscles, or the muscles of mastication, to be supplied by the motor root of the fifth. In addition, it supplies in part the platysma myoides. We have already seen that the buccal branch of the small root of the fifth is not distributed to the buccinator, but that this muscle is supplied exclusively by branches from the facial.[1]

Properties and Function of the Facial Nerve.—It has long been recognized that the facial is the motor nerve of the superficial muscles of the face, and that its division produces paralysis of motion and no marked effects upon sensation. It is evident, also, from the numerous communications of the facial with the fifth, that it probably contains in its course sensitive fibres. Indeed, all who have operated upon this nerve have found that it is slightly sensitive after it has emerged from the cranial cavity. It is a question, however, of great importance to determine, whether or not the facial be endowed with sensibility by virtue of its own fibres of origin. The main root is evidently from the motor tract, resembles the anterior roots of the spinal nerves, and is distributed to muscles; but this is joined by the intermediary nerve of Wrisberg, which presents a small enlargement, undoubtedly containing nerve-cells, somewhat analogous to the ganglia upon the posterior roots of the spinal nerves.

If the facial possess any sensibility at its root, it is but slight. In the early experiments of Sir Charles Bell, irritation of the facial exposed in an ass apparently produced no pain,[2] but the roots were not exposed in the cranial cavity. Magendie, on the other hand, in repeating these observations, found the nerve distinctly sensitive.[3] Longet, and

[1] See page 142.

[2] Bell, *On the Nerves*, etc.—*Philosophical Transactions*, London, 1821, Part i., pp. 413, 418.

[3] Magendie, *Journal de physiologie*, Paris, 1822, tome ii., p. 67, note.

most other experimenters, have also demonstrated the sensibility of the nerve after it has passed out of the cranial cavity,[1] except the inferior branch, in which Magendie and others have found no evidences of pain on irritating it in living animals.[2] Experiments have further shown that the facial derives its sensibility in greatest part from the fifth pair; for section of the latter within the cranial cavity has been found by Magendie to destroy the sensibility of the seventh.[3] It is probable, however, from other experiments, by Bernard, that the pain produced by section of the fifth interfered with the experiment, and that a part of the sensibility of the facial is derived from a communicating branch from the pneumogastric. Bernard exposed the facial, with this communicating branch, and found it sensitive; but after division of the branch from the pneumogastric, which produced considerable pain, the sensibility of the facial was destroyed.[4]

Direct observations upon the properties of the facial as it penetrates the auditory canal, and before it has received any anastomosing branches from sensitive nerves, must be to a certain extent unsatisfactory. All who have experimented upon the nerves know that the pain and depression which attend so serious an operation as that of exposing the roots of a nerve in the cranial cavity are sufficient to render it doubtful whether the parts be in a condition to exhibit a slight degree of sensibility, which the nerves may possess when perfectly normal. Magendie[5] and Bernard,[6] who have exposed the roots of origin of the facial, state unreservedly that they are absolutely insensible; but Longet very justly

[1] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 567.

[2] MAGENDIE, *Leçons sur les fonctions et les maladies du système nerveux*, Paris, 1841, tome ii., p. 181.

[3] MAGENDIE, *op. cit.*, p. 222.

[4] BERNARD, *Leçons sur la physiologie et la pathologie du système nerveux*, Paris, 1858, tome ii., p. 28.

[5] MAGENDIE, *Système nerveux*, Paris, 1841, tome ii., p. 208.

[6] BERNARD, *Système nerveux*, Paris, 1858, tome ii., p. 28.

remarks that the conditions under which such observations are made have not been, in his hands, sufficiently favorable to admit of a rigorous conclusion on this point.[1] The testimony of direct experimentation is in favor of the insensibility of the facial at its origin. It is true that the intermediary nerve of Wrisberg has a certain anatomical resemblance to the sensitive nerves, chiefly by virtue of its ganglioform enlargement; but direct experiments are wanting to show that it is actually sensitive. In view of this fact, it is impossible to reason conclusively from its anatomical characters alone.

The most convenient way to consider the functions of the facial will be to take up *seriatim* the properties and distribution of its different branches.

Functions of the Branches of the Facial within the Aqueduct of Fallopius.—The first branch, the large petrosal, is the motor root of Meckel's ganglion. This will be referred to again in connection with the sympathetic system. The second branch, the small petrosal, is one of the motor roots of the otic ganglion of the sympathetic. It is thought by Longet that this branch simply passes through the ganglion to be distributed to the tensor tympani muscle. This author regards the small petrosal and the tympanic branch of the facial as branches exclusively furnished by the intermediary nerve of Wrisberg, which he considers as the nerve of the tympanum, and has called the "tympanic motor nerve." This, however, is advanced as a mere supposition, not entirely proven by experiments.[2] The third branch, the tympanic, is distributed exclusively to the stapedius muscle. The second and third branches will be again considered in connection with the physiology of the internal ear.

According to the experiments of Savart,[3] paralysis of the

[1] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 567.

[2] Ibid., p. 579.

[3] SAVART, *Recherches sur les usages de la membrane du tympan et de l'oreille externe.—Journal de physiologie*, Paris, 1824, tome iv., p. 204.

tensor tympani should produce an increased susceptibility of the ear to ordinary sonorous vibrations. Contrary to what might be supposed, it is pretty certain that the membrane of the tympanum vibrates most intensely when it is relaxed, the vibration being much less when it is rendered tense by the action of the large muscle of the malleus. This view is accepted by Müller, who repeated and extended the experiments of Savart. Müller states that this is a physical law with regard to membranes of the extent of the tympanum.[1] It is farther carried out by certain cases of paralysis of the facial in the human subject, which present, among other symptoms, a painful sensibility of the ear to powerful impressions of sound. One of the earliest observed and most remarkable of these is the case of Prof. Roux, of Paris, who suffered from a temporary facial paralysis, and who noted that "the membrane of the tympanum was painfully sensible even to slight noises."[2] This symptom has often been noted in facial palsy.[3]

The fourth branch, the chorda tympani, is so important that it demands special consideration. The fifth branch is given off opposite to the origin of the chorda tympani and passes to the pneumogastric, to which nerve it probably supplies motor filaments. We have already seen, in studying the properties of the roots of the facial, that in this branch, sensory filaments pass from the pneumogastric and constitute a part of the sensory connections of the facial.[4]

Functions of the Chorda Tympani.—This branch passes between the bones of the ear and through the tympanic cavity to the lingual branch of the inferior maxillary division of the fifth, which it joins at an acute angle, between the pterygoid muscles. It has been a question whether this

[1] MÜLLER, *Elements of Physiology*, London, 1843, vol. ii., p. 1256.

[2] BELL, *The Nervous System*, London, 1844, p. 329.

[3] BERNARD, *Leçons sur la physiologie et la pathologie du système nerveux*, Paris, 1858, tome ii., p. 114.

[4] See page 153.

nerve be simply enclosed in the sheath of the lingual branch of the fifth or be so closely connected with it that it cannot be traced to a distinct distribution. Upon this point we are disposed to adopt the opinion of Sappey, who, as the result of minute dissections, regards the union as complete, "fibril to fibril." As regards the portion of the facial which furnishes the filaments of the chorda tympani, it is impossible to determine anatomically whether these come from the main root or from the intermediary nerve of Wrisberg, as the fibres of these roots are closely united before the chorda tympani is given off.[1]

Concerning the general properties of the chorda tympani, it is curious to note the opposite opinions of different physiologists; some regarding it as a motor nerve, others as purely sensitive, and others as a special nerve of taste. When we come to analyze the actual experimental observations upon the nerve, it is seen that it cannot be regarded as an ordinary motor nerve; for galvanization of the root of the facial before this branch is given off, and careful galvanization of the chorda tympani itself, produce not the slightest movement in the tongue.[2] The operative procedure necessary to expose the parts is so severe as to render observations with regard to its sensibility very unsatisfactory. It is certain, however, that it is not an acutely sensitive nerve like the fifth, or like certain branches of the pneumogastric.

The only questions that we propose to consider in this connection relate to the functions of the chorda tympani as a nerve of gustation, and as it influences the secretion of the submaxillary gland.

There can be no doubt with regard to the influence of the chorda tympani upon the sense of taste in the anterior portion of the tongue. Without citing all of the experiments and pathological observations bearing upon this ques-

[1] SAPPEY, *Traité d'anatomie*, Paris, 1852, tome ii., p. 258.

[2] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 581, note.

tion, it is sufficient to state, that in cases of disease or injury, in which the root of the facial is involved so that the chorda tympani is paralyzed, in addition to the ordinary phenomena of paralysis of the superficial muscles of the face, there is loss of taste in the anterior portion of the tongue on the side corresponding to the lesion. Numerous cases of this kind are quoted in works on physiology, which will be referred to more fully in connection with the subject of gustation.

In 1863, we had under observation, for several months, a soldier who received a gunshot-wound, the ball passing through the head, entering just above the ala of the nose on the left side and emerging behind the mastoid process of the right temporal bone. The wound was nearly healed while he was under observation, and the usual symptoms of complete facial paralysis were manifested on the right side. The buccinator and the orbicularis oculi were completely paralyzed. Vision in the right eye was slightly impaired, but was improving. The hearing was perfect, and there were no abnormal phenomena except those apparently due to injury of the facial. The sense of taste was entirely abolished in the anterior portion of the tongue on the right side. Experiments on this point were repeatedly made with salt, pepper, and other sapid substances. This patient was examined on one occasion by Prof. Dalton, and was exhibited in two successive years to the class at the Bellevue Hospital Medical College, when the above-mentioned facts were verified.

Physiologists have observed loss of taste in the anterior portion of the tongue, in dogs, cats, and other animals, following section of the root of the facial or of the chorda tympani. Some observers, it is true, have failed to note the phenomena satisfactorily, and there is some difference of opinion with regard to the real origin of the gustatory filaments; but the fact that the chorda tympani influences the taste can hardly be doubted. Adopting this view, we shall

defer the full consideration of the functions of the chorda tympani until we come to treat of the special sense of taste.

Schiff, in 1851, was the first to note the influence of the chorda tympani upon the secretion of the submaxillary gland. In some works on physiology, the experiments of Ludwig are referred to as the first upon this subject;[1] but Ludwig only noted the influence upon the salivary secretion, of filaments going to the submaxillary from the lingual branch of the fifth, without experimentally demonstrating their real origin.[2] In the experiments of Schiff, the chorda tympani was exposed and the flow of the submaxillary saliva noted. Upon division of the chorda tympani, the flow of saliva was momentarily increased, but was soon arrested; and subsequently, stimulation of the gustatory sense failed to induce secretion, as it does when the nerve is intact.[3] Similar experiments, on a much more extended scale, were made by Bernard, in the following way:

The duct of the submaxillary gland was exposed in a dog, and into it was fixed a silver canula. The nervous filaments going to the gland from the lingual branch of the fifth were then isolated. A little vinegar introduced into the mouth caused an abundant flow of saliva from the tube. The chorda tympani was then divided, by introducing a sharp instrument through the membrane into the tympanic cavity. After division of the nerve, the introduction of vinegar into the mouth failed to excite the salivary secretion. From this and similar experiments, Bernard concludes that the chorda tympani is the motor nerve of the submaxillary gland. After having arrested the secretion by section of the chorda tympani, the action of the gland was

[1] Longet, *Traité de physiologie*, Paris, 1869, tome iii., p. 582.

[2] Ludwig, *Neue Versuche über die Beihilfe der Nerven zur Speichelabzonderung.—Zeitschrift für rationelle Medicin*, Heidelberg, 1851, Neue Folge, Bd. i., S. 255, *et seq.*

[3] Schiff, *Leçons sur la physiologie de la digestion*, Florence et Turin, 1867, tome i., p. 217.

induced by galvanization of the peripheral end of the nerve.[1] Section of the facial after its passage out of the stylo-mastoid foramen did not arrest the action of the parotid; but section of the nerve within the cranium arrested the secretion, both of the parotid and submaxillary.[2]

These observations show conclusively that the facial, either through branches from its proper roots or its filaments of communication with other nerves, regulates the secretion of at least two of the salivary glands; a fact to which we have already alluded in another volume.[3]

Influence of Various Branches of the Facial upon the Movements of the Palate and Uvula.—There can be little doubt that filaments from the facial animate certain of the movements of the velum palati and uvula. It has been observed that, in certain cases of facial paralysis, the palate upon one side is perfectly flaccid and the uvula is drawn to the opposite side. Montault[4] cites a case of this kind, and a very striking example is given in full by Bernard;[5] but these phenomena do not occur unless the nerve be affected at its root or within the aquæductus Fallopii. It is true that the uvula is frequently drawn to one side or the other in persons unaffected with facial paralysis, as was observed by Debrou,[6] but it is none the less certain that it is deviated as a consequence of paralysis of the facial in some instances.[7] These facts, however, in the absence of direct experiments, do not show conclusively that the facial supplies the muscles of the soft palate.

[1] BERNARD, *Leçons sur la physiologie et la pathologie du système nerveux*, Paris, 1858, tome ii., p. 148, *et seq.*

[2] *Op. cit.*, p. 155.

[3] See vol. iii., Secretion, p. 31.

[4] MONTAULT, *Dissertation sur l'hémiplégie faciale*, *Thèse*, No. 300, Paris, 1831.

[5] BERNARD, *Leçons sur la physiologie et la pathologie du système nerveux*, Paris, 1858, tome ii., p. 133.

[6] DEBROU, *Thèses de l'école de médecine*, Paris, 1841, No. 266.

[7] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 576.

Direct experiments upon the roots of the facial have not been followed by uniform results. Debrou, in the thesis just referred to, mentions one experiment in which galvanization of the facial within the cranial cavity produced decided contraction of the muscles of the palate; but in four others, the results were negative. Nuhn, however, produced contractions of these muscles by galvanization of the nerve in the cranium in a man immediately after decapitation.[1] The experiments of Bernard upon this point are the most conclusive; but while they show, beyond a doubt, that the facial animates the movements of the soft palate, they do not indicate the course of the filaments from the nerve to the muscles. In these experiments, made in connection with M. Davaine, the whole of the velum palati was exposed in a large-sized dog, by cutting through the hyoid bone. The trunk of the glosso-pharyngeal nerve was then exposed in the neck, near its point of emergence at the posterior foramen lacerum, and the animal was killed by section of the spinal cord just below the origin of the cranial nerves. This being done, the glosso-pharyngeal was galvanized, which produced violent contractions of the velum, the pillars of the fauces, and a part of the pharynx, on one side. The nerve was then divided, and the galvanization applied to its peripheral end without producing any movement in the velum. The central end was then galvanized, when the contractions were as vigorous as when the nerve was intact. This result would lead to the supposition that contractions of the muscles of the palate following galvanization of the glosso-pharyngeal are reflex and not due to the direct action of filaments of distribution from this nerve. In a second experiment, the parts were exposed in the same way, and, in addition, the facial was divided upon the right side at its entrance into the internal auditory canal. The glosso-pharyn-

[1] NUHN, *Versuche an einem Enthaupteten nebst erläuternden Versuchen an Thieren.—Zeitschrift für rationelle Medicin*, Heidelberg, 1853, Neue Folge, Bd. iii., S. 129, *et seq.*

geal nerve was then galvanized upon the side on which the facial had been divided, with the effect of producing movements of the pillars of the fauces, but not of the velum palati itself. The glosso-pharyngeal was then galvanized upon the side on which the facial was intact, which produced movements of the velum the same as in the first experiment. Galvanization of the pneumogastric, the sublingual, and the lingual branch of the fifth, failed to produce movements of the velum.

"The first experiment proves that the glosso-pharyngeal nerve is not the motor nerve of the velum palati, but that it induces reflex movements by the excitation which it transmits to the nervous centre, an excitation which is carried to the parts by another nerve.

"The second experiment proves that the reflex movements of the velum palati, induced by the excitation of the glosso-pharyngeal, are in part transmitted by the facial nerve, the movements of the pillars not being produced by filaments belonging to this nerve." [1]

Bernard also noted a fact, which has sometimes been observed in cases of facial paralysis, that the point of the tongue is deviated after section of the facial; which is explained by the presence of a filament described by Hirschfeld, going from the facial to the tongue.

As we before remarked, the experiments of Bernard do not indicate the mode of communication between the facial and the muscles of the palate. Longet regards the filaments of the facial which influence the levator palati and azygos uvulæ muscles as derived from the large petrosal branch of the nerve, passing to the muscles through Meckel's ganglion, the filaments to the palato-glossus and the palato-pharyngeus being given off from the glosso-pharyngeal, but originally coming from an anastomosing branch of the facial. As regards the branches of communication from the glosso-

[1] BERNARD, *Leçons sur la physiologie et la pathologie du système nerveux*, Paris, 1858, tome ii., p. 178.

pharyngeal, Longet mentions a preparation by Richet, in the museum of the *École de médecine*, of Paris, in which branches of the facial on one side passed directly to the palato-glossus and the palato-pharyngeus without any connection with the glosso-pharyngeal nerve.[1] In our anatomical description of the branches of the facial, we have already noted a filament, described by Hirschfeld, which passes to the stylo-glossus and palato-glossus muscles.[2] This is the filament affected in deviation of the point of the tongue.

In view of the pathological examples of paralysis of the palate and uvula in certain cases of facial palsy, the frequent occurrence of contractions of the muscles of these parts upon galvanization of the facial, and the reflex action through the glosso-pharyngeal and the facial, there can be little doubt that the muscles of the palate and uvula are animated by filaments derived from the seventh nerve. The effects of paralysis of these muscles are manifested by more or less difficulty in deglutition and in the pronunciation of certain words, with great difficulty in the expulsion of mucus collected in the back part of the mouth and the pharynx. These points are well illustrated in the case of facial palsy, with paralysis of one side of the palate, cited by Bernard.[3]

Functions of the External Branches of the Facial.—The general function of the branches of the facial going to the superficial muscles of the face is sufficiently evident, in view of our present knowledge of the distribution of these branches and the general properties of the nerve. Throughout the writings of Sir Charles Bell, the facial is spoken of as the "respiratory nerve of the face." It is now recognized as the nerve which presides over the movements of the superficial muscles of the face, not including those directly concerned in the act of mastication. This being its general function, it

[1] LONGET, *op. cit.*, tome iii., p. 581. [2] See page 150.
[3] BERNARD, *op. cit.*, tome ii., p. 133.

is easy to assign to each of what may be termed the external branches of the facial its particular office.

Just after the nerve has passed out at the stylo-mastoid foramen, it sends to the glosso-pharyngeal the communicating branch, the functions of which we have just considered in connection with the movements of the palate.

The posterior auricular branch, becoming sensitive by the addition of filaments from the cervical plexus, gives sensibility to the integument on the back part of the ear and over the occipital portion of the occipito-frontalis muscle. It animates the retrahens and the attollens aurem, muscles but little developed in man, but very important in certain of the inferior animals. It also animates the posterior portion of the occipito-frontalis muscle.

The branches distributed to the posterior belly of the digastric and to the stylo-hyoid muscle simply animate these muscles, one of the uses of which is to assist in deglutition. The same may be said of the filaments that go to the stylo-glossus.

The two great branches distributed upon the face after the trunk of the nerve has passed through the parotid gland have the most prominent function. Both of these branches are somewhat sensitive from their connections with other nerves, and are distributed in small part to integument.

The temporo-facial branch animates all of the muscles of the upper part of the face. In complete paralysis of this branch, the eye is constantly open, even during sleep, from paralysis of the orbicularis muscle. In cases of long standing, the globe of the eye may become inflamed from constant exposure, from abolition of the movements of winking by which the tears are distributed over its surface and little foreign particles are removed, and, in short, from absence of the protective action of the lids. In these cases, the lower lid may become slightly everted. The frontal portion of the occipito-frontalis, the attrahens aurem, and the corrugator supercilii muscles, are also paralyzed. The most prominent

symptom of paralysis of these muscles is inability to corrugate the brow upon one side, as in frowning.

Paralysis of the muscles that dilate the nostrils has been shown to have an important influence upon respiration through the nose. It was the synchronism between the acts of dilatation of the nostrils and the movements of inspiration which first led Sir Charles Bell to regard the facial as a respiratory nerve. In instances of complete paralysis of the nostril of one side, there is frequently some difficulty in inspiration. Sir Charles Bell refers to a case in which, when "the patient lay with the sound side against the pillow, he was under the necessity of holding the paralytic nostril open with the fingers, in order to breathe freely."[1] In the horse, the movements of the nostrils are essential to respiration, the animal being unable to breathe through the mouth. When both facial nerves are divided in this animal, the nostrils collapse and are occluded with each effort at inspiration, and death takes place from suffocation.[2]

Sir Charles Bell[3] and others have also noted the interference with olfaction, due to the inability to inhale with one nostril, in cases of facial paralysis. The influence of the nerve in the act of conveying odorous emanations to the olfactory membrane is sufficiently evident after what we have remarked concerning the action of the facial in respiration.

The effects of paralysis of the other superficial muscles of the face are manifested in the distortion of the features, from the unopposed action of the muscles upon the sound side; a phenomenon which is sufficiently familiar to the prac-

[1] Bell, *The Nervous System of the Human Body*, London, 1844, p. 54. The case referred to is No. VI., in the Appendix; but this seems to be an error, as no such circumstance is mentioned in this case. Still the fact illustrated is not to be doubted.

[2] Bernard, *Leçons sur la physiologie et la pathologie du système nerveux*, Paris, 1858, tome ii., p. 38.

[3] Bell, *Of Smelling as influenced by the Portio Dura of the Seventh Nerve.—The Nervous System*, London, 1844, p. 134.

tical physician. When facial palsy affects one side and is complete, the angle of the mouth is drawn to the opposite side, the eye upon the affected side is widely and permanently opened, even during sleep, and the face has upon that side a peculiarly expressionless appearance. When a patient affected in this way smiles or attempts to grimace, the distortion is much increased. The lips are paralyzed upon one side, which sometimes causes a flow of saliva from the corner of the mouth. In the lower animals that use the lips in prehension, paralysis of these parts interferes considerably with the taking of food. The flaccidity of the paralyzed lips and cheek in the human subject sometimes causes a puffing movement with each act of expiration, as if the patient were smoking a pipe.

We have already seen that the buccinator is not supplied by filaments from the nerve of mastication, but is animated solely by the facial. Paralysis of this muscle interferes materially with mastication, from a tendency to accumulation of the food between the teeth and the cheek. Patients complain of this difficulty, and sometimes keep the food between the teeth by pressure with the hand. In the rare instances in which both facial nerves are paralyzed, there is very great difficulty in mastication from the cause just mentioned.

The functions of the external branches of the facial are thus sufficiently simple; and it is only as its deep branches affect the taste, the movements of deglutition, etc., that it is difficult to ascertain their exact office. As this is the nerve of expression of the face, it is in the human subject that the phenomena attending its paralysis are most prominent. When both sides are affected, the appearance is most remarkable, the face being absolutely expressionless and looking as if it had been covered with a mask.

CHAPTER VI.

SPINAL ACCESSORY AND SUBLINGUAL NERVES.

Spinal accessory nerve (third division of the eighth)—Physiological anatomy—Properties and functions of the spinal accessory—Functions of the internal branch from the spinal accessory to the pneumogastric—Influence of the spinal accessory over the vocal movements of the larynx—Influence of the internal branch of the spinal accessory upon deglutition—Influence of the spinal accessory upon the heart—Functions of the external, or muscular branch of the spinal accessory—Sublingual, or hypoglossal nerve (ninth)—Physiological anatomy—Properties and functions of the sublingual—Gloso-labial paralysis.

A DESCRIPTION of the properties and functions of the spinal accessory and the sublingual completes the physiological history of the motor nerves emerging from the cranial cavity. The functions of these nerves are important, and, in the case of the spinal accessory, possess considerable interest, from the fact that physiological investigations have, only within a few years, determined the significance of certain of its anatomical relations. As we have done in studying the other motor nerves, we will treat successively of their anatomical relations, general properties and functions.

Spinal Accessory Nerve. (*Third Division of the Eighth.*) —The spinal accessory nerve, from the remarkable extent of its origin, its important anastomoses with other nerves, and its curious course and distribution, has long engaged the attention of anatomists and physiologists, who have advanced many theories with regard to its office. We will content ourselves, however, with a simple description of its

anatomy as it appears from late researches, and will begin its physiological history with the comparatively recent experiments which have advanced our positive knowledge of its properties.

Physiological Anatomy.—The origin of this nerve is very extensive. A certain portion arises from the lower half of the medulla oblongata, and the rest takes its origin below, from the upper two-thirds of the cervical portion of the spinal cord. That portion of the root which arises from the medulla oblongata is called, by the French, the bulbar portion, the roots from the cord constituting the spinal portion. Inasmuch as there is a marked difference between the functions of these two portions, the anatomical distinction just mentioned is important.

The superior roots arise by four or five filaments from the lower half of the medulla oblongata below the origin of the pneumogastrics. These filaments of origin, in preparations hardened by prolonged immersion in alcohol, are shown to be connected with the lateral portion of the medulla, and not with the posterior columns. Their origin seems, therefore, to be from the motor tract.[1]

The spinal portion of the nerve arises from the upper part of the cervical division of the spinal cord, between the anterior and posterior roots of the upper four or five cervical nerves. The filaments of origin are from six to eight in number. The most inferior of these is generally single, the other filaments being frequently arranged in pairs. These take their origin from the lateral portion of the cord, rather nearer the posterior median line than the roots from the medulla oblongata.

Following the nerve from its most inferior filament of origin upward, it gradually increases in size by union with its other roots, enters the cranial cavity by the foramen magnum, and passes to the jugular foramen, by which it

[1] SAPPEY, *Traité d'anatomie descriptive*, Paris, 1852, tome ii., p. 298.

emerges, in connection with the glosso-pharyngeal, the pneumogastric, and the internal jugular vein.

In its course, the spinal accessory anastomoses with several nerves. Just as it enters the cranial cavity, it receives filaments of communication from the posterior roots of the upper two cervical nerves. These filaments, however, are not constant. It frequently, though not constantly, sends a few filaments to the superior ganglion, or ganglion of the root of the pneumogastric. After it has emerged by the jugular foramen, it sends a branch of considerable size to the pneumogastric, from which nerve it also receives a few filaments of communication. This branch will be again referred to in connection with the distribution of the nerve. In its course, it also receives filaments of communication from the anterior branches of the second, third, and fourth cervical nerves.

In its distribution, the spinal accessory presents two branches. The first, or anastomotic branch, passes to the pneumogastric just below the plexiform enlargement which is sometimes called the ganglion of the trunk of the pneumogastric.

The internal, or anastomotic branch, is composed principally, if not entirely, of the filaments that take their origin from the medulla oblongata. As it joins the pneumogastric, it subdivides into two smaller branches. The first of these forms a portion of the pharyngeal branch of the pneumogastric. The second becomes intimately united with the pneumogastric, lying at its posterior portion, and furnishes filaments to the inferior, or recurrent laryngeal branch, which is distributed to all of the muscles of the larynx except the crico-thyroid. The passage of the filaments from the spinal accessory to the pharyngeal branch of the pneumogastric is easily observed; but the fact that filaments from this nerve pass to the larynx by the recurrent laryngeal has been ascertained only by physiological experiments.

The external, or large branch of the spinal accessory,

called the muscular branch, penetrates and passes through the posterior portion of the upper third of the sterno-cleido-mastoid muscle, goes to the anterior surface of the trapezius, which muscle receives its ultimate branches of distribution. In its passage through the sterno-cleido-mastoid, it joins with branches from the second and third cervical nerves, and sends filaments of distribution to the muscle. Although the two muscles just mentioned receive numerous motor filaments from the spinal accessory, they are also supplied from the cervical nerves; and, consequently, they are not entirely paralyzed when the spinal accessory is divided.

Properties and Functions of the Spinal Accessory.—Notwithstanding the great difficulty in exposing and operating upon the roots of the spinal accessory, it has been demonstrated that their galvanization produces convulsive movements in certain muscles. The most satisfactory experiments with relation to the general properties of the roots were made by Bernard. This physiologist cut through the occipito-atloid membranes and galvanized the filaments within the spinal canal. By galvanizing the filaments arising from the medulla oblongata, he produced contractions of the muscles of the pharynx and larynx and no movements of the sterno-mastoid and trapezius. Galvanization of the roots arising from the spinal cord produced movements of the two muscles just mentioned, and absolutely no movements in the larynx.[1] Bernard has further shown that the roots of the nerve are endowed with recurrent sensibility from the posterior roots of the first three pairs of cervical nerves.[2] In view of these experiments, it is evident that the true filaments of origin of the spinal accessory are motor; and it is further evident that the filaments from

[1] BERNARD, *Recherches expérimentales sur les fonctions du nerf spinal*, p. 731. It is stated in a note that this memoir was printed in the *Archives de médecine*, in 1844.

[2] *Loc. cit.*, p. 730. We have already fully considered the subject of recurrent sensibility in the anterior roots of the spinal nerves (see page 81).

the medulla oblongata are distributed to the muscles of the pharynx and larynx, while the filaments from the spinal cord go to the sterno-cleido-mastoid and trapezius.

The trunk of the spinal accessory, after the nerve has passed out of the cranial cavity, is endowed with a certain degree of sensibility. If the nerve be divided, the peripheral extremity manifests the recurrent sensibility, but the central end is also sensible, probably from direct filaments of communication from the cervical nerves and the pneumogastric. As we have remarked, however, in treating of the properties of some other of the cranial nerves, it is exceedingly difficult to note satisfactorily a slight degree of sensibility in nerves that can be exposed only by a tedious and painful operation.

The functions of the external, or muscular branch of the spinal accessory are sufficiently evident; and the effects of the destruction of the nerves on both sides, as far as this branch is concerned, simply resolve themselves into the phenomena due to partial paralysis of the sterno-mastoid and trapezius; but the functions of the branch which joins the pneumogastric are much more complex. Without discussing the speculative views of the older anatomists and physiologists, we will commence with the experiments of Bischoff, which were the first to give us any definite ideas of the functions of the internal branch.

Functions of the Internal Branch from the Spinal Accessory to the Pneumogastric.—Bischoff attempted to ascertain the functions of this branch by dividing the roots of the spinal accessory on both sides in a living animal. The results of his experiments may be stated in a very few words. He attempted to divide all of the roots of the nerves on both sides by dissecting down to the occipito-atloid space and penetrating into the cavity of the spinal canal. In the first three experiments on dogs, the animals died so soon after section of the nerves, that no satisfactory results were

obtained. In two succeeding experiments on dogs, the animals recovered. After division of the nerves, the voice became hoarse; but a few weeks later, became normal. On killing the animals, an examination of the parts showed that some of the filaments of origin had not been divided. An experiment was then made upon a goat, but this was unsatisfactory, as the roots were not completely divided. Finally, another experiment was made upon a goat. In this, the results were most satisfactory. After division of the nerve upon one side, the voice became hoarse. As the filaments were divided upon the opposite side, the voice was enfeebled, until finally it became extinct. The sound emitted afterward was one which could in nowise be called voice, "*qui neutiquam vox appellari potuit.*"[1] This experiment was made in the presence of Tiedemann and Seubertus, and was not repeated.

It is evident to any one familiar with the elaborate researches of Bernard upon the spinal accessory, that it was only necessary to confirm the single successful experiment of Bischoff to settle the fact of the influence of this nerve upon phonation. The great difficulty of the operative procedure, however, prevented its repetition on an extended scale. Longet, in 1841,[2] published an account of some experiments confirming, to a certain extent, those of Bischoff; but in his treatise on the nervous system, published in 1842,[3] he does not seem to regard the spinal accessory as the exclusive nerve of phonation, as he does in his work on physiology, published after the experiments of Bernard.[4] The results of the experiments performed at this time by Longet

[1] BISCHOFF, *Nervi Accessorii Willisii Anatomia et Physiologia*, Darmstadii, 1832, p. 94.

[2] LONGET, *Recherches expérimentales sur les fonctions des nerfs, des muscles du larnyx et sur l'influence du nerf accessoire de Willis dans la phonation.—Gazette médicale*, Paris, 1841, 2ème série, tome ix., p. 472.

[3] LONGET, *Anatomie et physiologie du système nerveux*, Paris, 1842, tome ii., p. 263.

[4] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 516.

were by no means so satisfactory as the single successful observation of Bischoff. In his memoir on the spinal accessory, Bernard gives full credit to Bischoff, and quotes from this author the very words we have just cited. With regard to the question of priority in the description of the function of this nerve in phonation, there can be no doubt concerning the accuracy of the experiment of Bischoff and its correct interpretation, in 1832. He demonstrated that the nerve presiding over the voice is the spinal accessory; although the fact rested on a single successful experiment, and was not accepted by physiologists before it had been fully confirmed by the repeated and conclusive experiments of Bernard, made by an entirely different method. To Bernard, however, remains, as we shall presently see, the merit of having demonstrated that the vocal muscles are supplied by those filaments of the spinal accessory that take their origin from the medulla oblongata.

Bernard, whose ingenious experiments determined exactly the influence of the spinal accessory over the vocal movements of the larynx, first repeated the experiments of Bischoff; but the animals operated upon died so soon, from hæmorrhage, or other causes, that his observations were not satisfactory.[1] After many unsuccessful trials, he succeeded in overcoming all difficulties, by following the trunk of the nerve back to the jugular foramen, seizing it here with a strong pair of forceps, and drawing it out by the roots.[2] This operation is difficult, but we have sev-

[1] BERNARD, *Recherches expérimentales sur les fonctions du nerf spinal*, p. 733. Bernard considers that death is due after this operation, as performed by Bischoff, to the passage of air into the veins.

[2] The operative procedure employed by Bernard is the following: The trunk of the nerve is exposed as it passes through the sterno-cleido-mastoid muscle. It is then followed up by careful dissection, avoiding blood-vessels as much as possible, to the posterior foramen lacerum, when the sublingual is seen crossing the course of the pneumogastric. It is here that the anastomotic branch leaves the spinal accessory to go to the pneumogastric. At this point, the external branch, with the anastomosing branch, is seized with a pair of rather broad-billed forceps, and gentle but firm traction is applied to the entire

eral times performed it with entire success, and verified, in every regard, the facts observed by Bernard. Within the last year, the excellent assistant to the chair of Physiology at the Bellevue Hospital Medical College, Dr. C. F. Roberts, has succeeded in extirpating these nerves for class-demonstrations. The operation is generally most successful in cats, though Bernard has succeeded frequently in other animals.

When one spinal accessory is extirpated, the vocal sounds are hoarse and unnatural. When both nerves are torn out, in addition to the disturbance of deglutition and the partial paralysis of the sterno-mastoid and trapezius muscles, the voice becomes extinct. Animals operated upon in this way move the jaws and make evident efforts to cry, but no vocal sound is emitted. This condition is very striking; and inasmuch as Bernard has kept animals, with both nerves extirpated, for months, the question of the function of these nerves in phonation may now be regarded as definitively settled.

It remains now to consider the experimental facts with regard to the influence of the different filaments of origin of the spinal accessory on the voice. These are simple, and entirely conclusive; and they are due exclusively to the researches of Bernard. This experimenter found that division of the roots of origin from the spinal cord not only did not affect the voice, but sometimes seemed to render it clearer; but that division of the roots of origin from the medulla oblongata abolished the voice, though the inferior roots were intact.[1]

It is not necessary to discuss the action of the muscles of the larnyx in phonation, as this subject has already been considered in full in another volume.[2] The beautiful experi-

nerve. Soon there is a cracking sensation conveyed to the hand as the roots give way, and the nerve may then be drawn out entire. With care, either the filaments of origin from the medulla or those from the cord may be extirpated alone.—(BERNARD, *op. cit.*, p. 736; and, *Leçons sur la physiologie et la pathologie du système nerveux*, Paris, 1858, tome ii., p. 296.)

[1] *Op. cit.*, p. 735.

[2] See vol. i., Voice and Speech, p. 490, *et seq.*

ments that have demonstrated the influence of the spinal accessory nerve over these muscles have pointed out the destination of the fibres that join the pneumogastric, which could never have been done so satisfactorily by dissection. They have shown further that the movements involved in phonation are more or less independent of the respiratory movements of the larnyx.

If the larnyx be exposed in a living animal, with all its nervous connections intact, it will be seen to open widely during inspiration, being passive in expiration. The wide opening of the glottis at this time is due to the fact that, after the operation, respiration is usually more or less labored; but if we carefully observe the parts when the respiratory acts are perfectly tranquil, the movements of the glottis seem to be very slight. The larynx is then permanently opened to a moderate degree, but the chink of the glottis is slightly dilated with each expiration. If the recurrent laryngeal nerves, which are distributed to all of the muscles of the larynx except the crico-thyroid, be now divided upon both sides, the larynx is entirely paralyzed, and in cats and young animals, in which the cartilages are soft and flexible, the parts are occluded by the effort of inspiration, and death takes place from suffocation. Of course the division of the recurrent laryngeal nerves abolishes the voice, but it arrests the other movements of the larynx as well. The distinction thus established between the action of the spinal accessory and the recurrent laryngeal nerves was fully illustrated by Bernard, in the following experiments:

In a cat, in which the voice had been completely destroyed by extirpation of both spinal accessory nerves, the larynx was exposed. The glottis was seen dilated so as to permit the free passage of air in respiration. The mucous membrane retained its sensibility, and when the interior of the larynx was irritated, a very slight but ineffectual effort was made to close the glottis. It was impossible for the animal to approximate the posterior points of attachment of

the vocal cords, or to put the cords on the stretch. If such irritation be applied to the larynx of an animal with the spinal accessory nerves intact, the glottis is instantly and firmly closed.[1]

In a cat about five weeks old, both spinal accessory nerves were extirpated, and the voice was thus destroyed. Two days after, both recurrent laryngeal nerves were divided, and the animal died almost immediately of suffocation.[2]

These experiments show conclusively that the internal, or communicating branch of the spinal accessory is the nerve which presides over the movements of the larynx in phonation. The filaments undoubtedly pass to the larynx in greatest part through the recurrent laryngeal branches of the pneumogastric; but the recurrent laryngeals also contain motor filaments from other sources, which are chiefly concerned in the respiratory movements of the glottis.

Influence of the Internal Branch of the Spinal Accessory upon Deglutition.—We must refer again to the experiments of Bernard for an account of the influence of the spinal accessory upon deglutition. There are two ways in which deglutition is affected through this nerve: 1. When the larynx is paralyzed as a consequence of extirpation of both nerves, the glottis cannot be completely closed to prevent the entrance of foreign bodies into the air-passages. In rabbits particularly, it was noted that particles of food penetrated the trachea and found their way into the lungs.[3] 2. The spinal accessory furnishes numerous filaments to the pharyngeal branch of the pneumogastric, and, through this nerve, directly affects the muscles of deglutition; but the muscles animated in this way by the spinal accessory have a

[1] BERNARD, *op. cit.*, p. 745.

[2] *Loc. cit.*, p. 749.

[3] BERNARD, *Leçons sur la physiologie et la pathologie du système nerveux*, Paris, 1858, tome ii., p. 323.

tendency to draw the lips of the glottis together, while they assist in passing the alimentary bolus into the œsophagus. When these important acts are wanting, there is some difficulty in the process of deglutition itself as well as danger of the passage of alimentary particles into the larynx.

Influence of the Spinal Accessory upon the Heart.—When we come to study the varied functions of the pneumogastrics, we will discuss fully the mechanism by which the contractions of the heart are arrested by galvanization of both of these nerves in the neck. A very curious and interesting observation by Waller has demonstrated that this influence, whatever be its mechanism, is derived from the spinal accessory, and necessarily comes through its communicating branch. It has been found that a powerful current of galvanism passed through the pneumogastric on one side will arrest the action of the heart. Waller found that if he extirpated the spinal accessory on one side, the action of the heart could not be arrested by galvanizing the pneumogastric upon the same side; but this result followed galvanization of the pneumogastric upon the opposite side, on which the connections with the spinal accessory were intact. These phenomena, however, could not be observed until from ten to twelve days had elapsed after the extirpation of the spinal accessory.[1] We have already seen, in treating of the general properties of the nerves, that the irritability of the motor nerves disappears in about four days after their separation from the nerve-centres.[2] In the observation just referred to, it seemed necessary that a sufficient time should elapse after extirpation of the spinal accessory for the irrita-

[1] WALLER, *Expériences sur les nerfs pneumogastriques et accessoires de Willis.*—*Gazette médicale*, Paris, 1856, 3ème série, tome xi., p. 420.

In these experiments, Waller demonstrated by microscopical examination the disorganization of both branches of the spinal accessory, and showed that their galvanization produced little, if any contraction in the muscles to which these branches were distributed.

[2] See p. 96.

bility of the filaments that join the pneumogastric to become extinct; but the experiment is sufficient to show the direct inhibitory influence of the spinal accessory on the heart. The subject will be more fully considered, however, in connection with the functions of the pneumogastrics.

Functions of the External, or Muscular Branch of the Spinal Accessory.—The most interesting feature in the recent researches into the functions of the spinal accessory is, that experimentalists have been able to separate physiologically the internal from the external branch. Observations have conclusively demonstrated that the internal branch, and the internal branch only, is directly concerned in the vocal movements of the larynx, and, to a great extent, in the closure of the glottis during deglutition. It has been noted, in addition, that animals in which both branches have been extirpated present irregularity of the movements of the anterior extremities and suffer from shortness of breath after violent muscular exertion. The use of the corresponding extremities in the human subject is so different, that it is not easy to make a direct application of these experiments; still, we can draw from them certain inferences with regard to the functions of the external branch in man.

In prolonged vocal efforts, the vocal cords are put upon the stretch, and the act of expiration is very different from that in tranquil breathing. In singing, for example, the shoulders are frequently fixed; and this is done to some extent by the action of the sterno-cleido-mastoid and the trapezius. We may suppose, then, that the action of the branch of the spinal accessory which goes to these muscles has a certain synchronism with the action of the branch going to the larynx and the pharynx; the one fixing the upper part of the chest so that the expulsion of the air through the glottis may be more nicely regulated by the expiratory muscles, and the other acting upon the vocal cords.[1]

[1] It is unnecessary to make any further reference in detail to the admirable

In what is known to physiologists as muscular effort, the mechanism of which has been discussed in another volume,[1] the glottis is closed, the thorax is fixed after a full inspiration, and respiration is arrested so long as the effort, if it be not too prolonged, is continued. The same synchronism, therefore, obtains in this as in prolonged vocal efforts. In experiments in which the muscular branch only has been divided, shortness of breath, after violent muscular effort, is observed; and this is probably due to the want of synchronous action of the sterno-cleido-mastoid and trapezius. The irregularity in the movements of progression in animals, in which either both branches or the muscular branches alone have been divided, is due to anatomical peculiarities. Bernard has observed these irregularities in the dog and the horse, but they are not so well marked in the cat. There have been no opportunities for illustrating these points in the human subject.

Sublingual, or Hypoglossal Nerve (Ninth).

The last of the motor cranial nerves is the sublingual; and its functions are intimately connected with the physiology of the tongue in deglutition and articulation, though it is also distributed to certain of the muscles of the neck.

Physiological Anatomy.—The apparent origin of the sublingual is from the medulla oblongata, in the groove between the olivary body and the anterior pyramid, on the line of the anterior roots of the spinal nerves. At this point, its root is formed of from ten to twelve filaments, which extend from the inferior portion of the olivary body to about the junction of the upper with the middle third. These filaments of origin are separated into two groups, superior and inferior. From this apparent origin, the filaments have been traced

memoir of Bernard on the spinal accessory, in which the function of the external branch in the lower animals has been fully investigated by experiments.

[1] See vol. iii., Movements, p. 477.

into the gray matter of the floor of the fourth ventricle, between the deep origin of the pneumogastric and the glosso-pharyngeal. Though there is much difference of opinion upon this point, it is probable, from the elaborate researches of Dr. Dean,[1] that some of the filaments of origin of these nerves decussate in the floor of the fourth ventricle.

The superior and inferior filaments of origin of the nerve unite respectively to form two bundles, which pass through distinct perforations in the dura mater. These two bundles then pass into the anterior condyloid foramen, and unite into a single trunk as they emerge from the cranial cavity. In some of the inferior animals, the calf, horse, pig, rabbit, dog, and cat, there is a delicate filament arising from the latero-posterior portion of the medulla, remarkable by the presence of a small ganglion, which joins the trunk of the nerve as it passes through the foramen. This was described by Mayer, and more lately by Vulpian; both of these observers having noted it exceptionally in the human subject.[2] Direct experiments are wanting to show positively the physiological properties of this ganglionic root.

After the sublingual has passed out of the cranial cavity, it anastomoses with several nerves. It sends a filament of communication to the sympathetic as it branches from the superior cervical ganglion. Soon after it has passed through the foramen, it sends a branch to the pneumogastric. It anastomoses by two or three branches with the upper two cervical nerves, the filaments passing in both directions between the nerves. It anastomoses with the lingual branch of the fifth, by two or three filaments passing in both directions.

In its distribution, the sublingual presents several remarkable peculiarities.

Its first branch, the descendens noni, passes down the

[1] DEAN, *The Gray Substance of the Medulla Oblongata and Trapezium*, Washington, 1864, p. 16.

[2] VULPIAN, *Sur la racine postérieure ou ganglionnaire du nerf hypoglosse.—Journal de la physiologie*, Paris, 1862, tome v., p. 5, *et seq.*

neck to the sterno-hyoid, sterno-thyroid, and omo-hyoid muscles. From its relations with important vessels and nerves, this branch possesses considerable surgical interest.

The thyro-hyoid branch is distributed to the muscle of the same name.

The other branches are distributed to the stylo-glossus, hyo-glossus, genio-hyoid, and genio-hyo-glossus muscles, their terminal filaments going to the intrinsic muscles of the tongue.

It is thus seen that the sublingual nerve is distributed to all of the muscles in the infra-hyoid region, the action of which is to depress the larynx and the hyoid bone after the passage of the alimentary bolus through the pharynx; to one of the muscles in the supra-hyoid region, the genio-hyoid; to most of the muscles which move the tongue; and to the muscular fibres of the tongue itself. The action of these muscles and of the tongue itself in deglutition has already been fully discussed in another volume.[1]

Properties and Functions of the Sublingual.—There is every reason to believe that the sublingual nerve is entirely insensible at its origin from the medulla oblongata. The fact that it arises from a continuation of the motor tract of the spinal cord and has no ganglion upon its main root would lead to the supposition that it is an exclusively motor nerve. In operating upon the roots of the spinal accessory, when the origin of the sublingual is necessarily exposed, Longet has irritated the roots in the dog without any evidence of pain on the part of the animal.[2] In the dog, Vulpian has constantly found the small ganglionic root,[3] which we have already mentioned as exceptional in the human subject. Such experiments, taken in connection with the anatomical characters of the nerve, render it almost cer-

[1] See vol. ii., Digestion, p. 189, *et seq.*

[2] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 584.

[3] VULPIAN, *Sur la racine postérieure ou ganglionnaire du nerf hypoglosse.—Journal de la physiologie*, Paris, 1862, tome v., p. 7.

tain that the main root is devoid of sensibility. They do not, however, positively demonstrate the insensibility of the ganglionic root, for a severe operation, it is well known, may temporarily abolish the sensibility of nerves when this is not very acute, as is seen in experiments upon the recurrent sensibility of the anterior roots of the spinal nerves. Still, as this filament is ordinarily absent in the human subject, there can be little doubt that the sublingual at its origin is exclusively motor.

All modern experimenters have confirmed the observations of Mayo[1] and of Magendie,[2] with regard to the sensibility of the sublingual after it has passed out of the cranial cavity. The anastomoses of this nerve with the upper two cervical nerves, the pneumogastric, and the lingual branch of the fifth, afford a ready explanation of this fact. According to Bernard, this nerve possesses recurrent sensibility derived from the fifth pair.[3]

The functions of the sublingual have already been so fully considered under the head of deglutition, that they need not be discussed elaborately in this connection. We will here simply state the phenomena which follow stimulation of the nerve and the division of both nerves in living animals.

The sublingual may be easily exposed in the dog by making an incision just below the border of the lower jaw, dissecting down to the carotid artery, and following the vessel upward until we see the nerve as it crosses its course. On applying a feeble current of galvanism at this point, there are evidences of sensibility, and the tongue is moved convulsively at each stimulation.

The phenomena following section of both sublingual

[1] MAYO, *Anatomical and Physiological Commentaries*, Number ii., London, 1823, p. 11.

[2] MAGENDIE, *Leçons sur les fonctions et les maladies du système nerveux*, Paris, 1841, tome ii., p. 290.

[3] BERNARD, *Leçons sur la physiologie et la pathologie du système nerveux*, Paris, 1858, tome ii., p. 241.

nerves point directly to their function. The most notable fact observed after this operation is, that the movements of the tongue are entirely lost, while the tactile and gustatory senses are not affected. These phenomena have been accurately described by Mayo,[1] Panizza,[2] Magendie,[3] and many others. Perhaps the most varied experiments made upon animals are those of Panizza. These have been fully detailed in connection with the subjects of mastication and deglutition. They consist simply in loss of power over the tongue, with considerable difficulty in deglutition. We have repeatedly noted all of these points and demonstrated them to medical classes.

In the human subject, the sublingual is usually more or less affected in hemiplegia. In these cases, as the patient protrudes the tongue, the point is deviated. This is due to the unopposed action of the genio-hyo-glossus upon the sound side, which, as it protrudes the tongue, directs the point toward the side affected with paralysis.

A disease of rather rare occurrence has lately been described under the name of glosso-labial paralysis, which is characterized by paralysis of the sublinguals, affecting also the orbicularis oris, and frequently the intrinsic muscles of the larynx. The phenomena referable to the loss of power over the tongue correspond to those observed in animals after section of the nerves. Patients affected in this way experience difficulty in deglutition, and, in addition, we note an interference with articulation, which cannot be observed in experiments upon animals. We lately had a case of this disease under observation in the Bellevue Hospital, the phenomena of which were peculiarly interesting from a physiological point of view. This patient presented complete paralysis of the tongue, with considerable difficulty in deglutition, probably from the tongue-affection. The orbicularis

[1] *Loc. cit.*

[2] PANIZZA, *Nouvelles recherches expérimentales sur les nerfs.—Gazette médicale*, Paris, 1835, p. 419. [3] *Loc. cit.*

oris was also paralyzed. The paralysis probably extended to the intrinsic muscles of the larynx, as little or no vocal sound could be made. The patient was incapable of articulate language, and communicated entirely by signs.

CHAPTER VII.

TRIFACIAL, OR TRIGEMINAL NERVE.

Physiological anatomy of the trifacial—Properties and functions of the trifacial—Division of the trifacial within the cranial cavity—Immediate effects of division of the trifacial—Remote effects of division of the trifacial—Effects of division of the trifacial upon the organs of special sense—Division of the trifacial before and behind the ganglion of Gasser—Communication with the sympathetic at the ganglion of Gasser—Explanation of the phenomena of disordered nutrition after division of the trifacial—Cases of paralysis of the trifacial in the human subject.

A SINGLE nerve, the large root of the fifth pair, called the trifacial, or the trigeminal, gives general sensibility to the face and the head as far back as the vertex. This is one of the most interesting of the cranial nerves, and is one of the first that was experimented upon by physiologists. It is interesting, not only as the great sensitive nerve of the face, but from its connections with other nerves and its relations to the organs of special sense. In studying the physiology of this nerve, we must necessarily begin with its physiological anatomy.

Physiological Anatomy.—The apparent origin of the large root of the fifth is from the lateral portion of the pons Varolii, posterior and inferior to the origin of the small root, from which it is separated by a few transverse fibres of white substance. The deep origin is far removed from its point of emergence from the encephalon. The roots pass entirely through the substance of the pons, from without inward and from before backward, without any connection with the fibres of the pons itself. By this course it reaches the me-

dulla oblongata, where the roots divide into three bundles. The anterior bundle passes from behind forward, between the anterior fibres of the pons and the cerebellar portion of the restiform bodies, to anastomose with the auditory nerve.[1] The other bundles, which are posterior, pass, the one in the anterior wall of the fourth ventricle to the lateral tract of the medulla oblongata, and the other, becoming grayish in color, to the restiform bodies, from which they may be followed as far as the point of the calamus scriptorius. According to Vulpian, a few fibres from the two sides decussate in the median line in the anterior wall of the fourth ventricle.[2]

From this origin, the large root of the fifth passes obliquely upward and forward to the ganglion of Gasser, which is situated in a depression in the petrous portion of the temporal bone on the internal portion of its anterior face.

The Gasserian ganglion is semilunar in form (sometimes it is called the semilunar ganglion), with its concavity looking upward and inward.[3] At the ganglion, the nerve receives filaments of communication from the carotid plexus of the sympathetic. This anatomical point is of importance in view of some of the remote effects which follow division of the fifth nerve through the ganglion in living animals.

It will be necessary only to describe in a general way

[1] LUDOVIC HIRSCHFELD, *Système nerveux*, Paris, 1866, p. 166. The anastomosis of the auditory nerve has been denied (VULPIAN, *Essai sur l'origine de plusieurs paires des nerfs craniens*, *Thèse*, Paris, 1853, p. 27), but it is admitted by most anatomists.

[2] *Op. cit.*, p. 25.

[3] The structure of this ganglion was first recognized by Gasser, Professor of Anatomy in Vienna. His observations, however, were published by Hirsch, a pupil of Gasser, in 1765 (HIRSCH, *Paris quinti Nervorum encephali*, Viennæ, 1765, in LUDWIG, *Scriptores Nevrologici minores selecti*, Lipsiæ, 1791, tomus i., p. 244, *et seq.*). Hirsch first gave it the name of Gasserian ganglion (p. 262). Some authors call it the Casserian ganglion, probably confounding Gasser with Casserius. Casserius, in his anatomical figures, describes many parts of the brain and nerves, but says nothing of the ganglion of the fifth (CASSERIUS, *Anatomiche Tafeln*, Franckfurt am Mayn, 1756).

the numerous branches of distribution of the fifth nerve, remembering that it is the great sensitive nerve of the face.

At the ganglion of Gasser, from its anterior and external portion, are given off a few small and unimportant branches to the dura mater and tentorium.

From the convex border of the ganglion, the three great branches arise that have given to the nerve the name of trifacial or trigeminal. These are: 1, the ophthalmic; 2, the superior maxillary; 3, the inferior maxillary. The ophthalmic and the superior maxillary branch are derived entirely from the sensory root. The inferior maxillary branch joins with the motor root and forms a mixed nerve.

The ophthalmic branch, the first division of the fifth, is the smallest of the three. Before it enters the orbit, it receives filaments of communication from the sympathetic, sends small branches to all of the motor nerves of the eyeball, and gives off a small recurrent branch which passes between the layers of the tentorium.

Just before the ophthalmic branch enters the orbit by the sphenoidal fissure, it divides into three branches; the lachrymal, frontal, and nasal.

The lachrymal, the smallest of the three, sends a branch to the orbital branch of the superior maxillary nerve, passes through the lachrymal gland, to which certain of its filaments are distributed, and its terminal filaments go to the conjunctiva and the integument of the upper eyelid.

The frontal branch, the largest of the three, divides into the supra-trochlear and supra-orbital nerves. The supra-trochlear passes out of the orbit between the supra-orbital foramen and the pulley of the superior oblique muscle. It sends in its course a long, delicate filament to the nasal branch, and is finally lost in the integument of the forehead. The supra-orbital passes through the supra-orbital foramen, sends a few filaments to the upper eyelid, and supplies the forehead, the anterior and median portions of the scalp, the

mucous membrane of the frontal sinus, and the pericranium covering the frontal and parietal bones.

The nasal branch, before it penetrates the orbit, gives off a long, delicate filament to the ophthalmic ganglion, constituting its sensory root. It then gives off the long ciliary nerves, which pass to the ciliary muscle and iris. Its trunk then divides into the external nasal, or infra-trochlearis, and the internal nasal, or ethmoidal. The infra-trochlearis is distributed to the integument of the forehead and nose, to the internal surface of the lower eyelid, the lachrymal sac, and the caruncula. The internal nasal is distributed to the mucous membrane, and also in part to the integument of the nose.

The superior maxillary branch of the fifth passes out of the cranial cavity by the foramen rotundum, traverses the infra-orbital canal, and emerges upon the face by the infra-orbital foramen. Branches from this nerve are given off in the spheno-maxillary fossa and the infra-orbital canal, before it emerges upon the face. In the spheno-maxillary fossa, the first branch is the orbital, which passes into the orbit, giving off one branch, the temporal, which passes through the temporal fossa by a foramen in the malar bone, and is distributed to the integument on the temple and the side of the forehead; another branch, the malar, which likewise emerges by a foramen in the malar bone, is distributed to the integument over this bone. In the spheno-maxillary fossa, are also given off two branches, which pass to the spheno-palatine, or Meckel's ganglion. From this portion of the nerve, branches are given off, the two posterior dental nerves, which are distributed to the molar and bicuspid teeth, the mucous membrane of the corresponding alveolar processes, and to the antrum.

In the infra-orbital canal, a large branch, the anterior dental, is given off to the teeth and mucous membrane of the alveolar processes not supplied by the posterior dental nerves. This nerve anastomoses with the posterior dental.

The terminal branches upon the face are distributed to

the lower eyelid (the palpebral branches); to the side of the nose (the nasal branches), anastomosing with the nasal branch of the ophthalmic; and to the integument and mucous membrane of the upper lip (the labial branches).

The inferior maxillary is a mixed nerve, composed of the inferior division of the large root and the small root. The distribution of the motor filaments has already been described under the head of the nerve of mastication.[1] This nerve passes out of the cranial cavity by the foramen ovale, and then separates into the anterior division, containing nearly all of the motor filaments, and the posterior division, which is chiefly sensory. The sensory portion breaks up into numerous branches:

1. The auriculo-temporal nerve supplies the integument in the temporal region, the auditory meatus and the integument of the ear, the temporo-maxillary articulation, and the parotid gland. It also sends important branches of communication to the facial.

2. The lingual branch is distributed to the mucous membrane of the tongue as far as the point, the mucous membrane of the mouth, the gums, and to the sublingual gland. This nerve receives an important branch from the facial, the chorda tympani, which has already been described.[2] From this nerve, also, are given off two or three branches which pass to the submaxillary ganglion, constituting its sensory roots.

3. The inferior dental nerve, the largest of the three, passes in the substance of the inferior maxillary bone, beneath the teeth, to the mental foramen, where it emerges upon the face. The most important sensory branches are those which supply the pulps of the teeth, and the branches upon the face. The nerve, emerging upon the face by the mental foramen, called the mental nerve, supplies the integument of the chin and the lower part of the face, the lower lip, and sends certain filaments to the mucous membrane of the mouth.

[1] See page 141. [2] See page 143.

Properties and Functions of the Trifacial.—Our definite knowledge with regard to the properties and functions of the large root of the fifth nerve dates from the experiments by Mayo, published in 1822. It is generally stated by authors that the researches of Sir Charles Bell, in 1811, led naturally to the idea that the ganglionic root of the fifth was entirely sensory. We have already shown, by full references to the paper printed by Sir Charles Bell, in 1811, that he therein attributed both motion and sensation to the anterior roots of the spinal nerves, regarding the ganglionic roots as nerves presiding over the functions of organic life.[1] The mistake made by authors in attributing the exact distinction between the functions of the large root of the fifth and the small root and the facial arises from the fact that a paper published originally in the Philosophical Transactions, in 1821,[2] is reprinted with other memoirs, "with some additional explanations."[3] The additions to the original paper are in such a form as to lead the reader to suppose that the author regarded the large root of the fifth as exclusively sensory; but, in the original paper, which we have carefully compared with the reprint, the distinction between the motor and the sensory root of the fifth is by no means clearly made.

In 1822, Herbert Mayo published an account of "experiments to determine the influence of the portio dura of the seventh, and of the facial branches of the fifth pair of nerves." These experiments consisted in dividing the infra-orbital, inferior maxillary, and frontal branches of the fifth, and the branch from the fifth to the seventh, in asses, by which it was demonstrated that these were exclusively sensory nerves.[4] In a second publication, the following year, it is

[1] See page 71.

[2] Bell, *On the Nerves; giving an Account of some Experiments on their Structure and Functions, which lead to a New Arrangement of the System.—Philosophical Transactions*, London, 1821, Part i., p. 398.

[3] Bell, *The Nervous System of the Human Body, as explained in a Series of Papers read before the Royal Society of London*, London, 1844, p. 33.

[4] Mayo, *Anatomical and Physiological Commentaries*, Number i., London, 1822, p. 107, *et seq.*

stated that the root of the fifth was divided in the cranial cavity in pigeons;[1] but this was with reference chiefly to the movements of the iris, though Mayo notes that after division of the nerve "the surface of the eyeball appears to have lost its feeling."

In 1823, Fodéra published an account of experiments in which he had divided the roots of the fifth in living animals (rabbits) by introducing a small knife through an opening in the parietal bone, along the base of the skull, and cutting through the roots near the Gasserian ganglion. The operation was followed by complete loss of sensibility upon the side on which the nerve had been divided.[2] In this and other experiments, however, the animals died a short time after the operation. The paper was presented to the Academy of Sciences, December 31, 1822, and was published at about the same time as the experiments of Mayo.

In 1824, Magendie published an account of his experiments on the fifth pair.[3] He divided the nerve at its root, by introducing a small stylet through the skull, and noted immediate loss of sensibility on the corresponding side of the face. Magendie was the first to succeed in keeping the animals alive, observing certain interesting remote effects of division of the nerve.

The operative procedure employed by Magendie has been followed, with great success, by other physiologists, particularly Bernard, to whose researches we are indebted for many additional facts of interest concerning the functions of the fifth nerve. As this is an operation which we have frequently performed with success, following the mi-

[1] Mayo, *Anatomical and Physiological Commentaries*, Number ii., London, 1823, p. 5.

[2] Fodéra, *Recherches expérimentales sur le système nerveux.—Journal de physiologie*, Paris, 1823, tome iii., p. 207.

[3] Magendie, *De l'influence de la cinquième paire de nerfs sur la nutrition et les fonctions de l'œil.—Journal de physiologie*, Paris, 1824, tome iv., p. 176, *et seq.;* and, *Suite des expériences sur les fonctions de la cinquième paire*, Ibid., p. 302, *et seq.*

nute directions laid down by Bernard, we will quote from him in brief the different steps.

The nerve may be divided in the cranial cavity with tolerable certainty in rabbits, cats, dogs, and Guinea-pigs, but it is most easily done in rabbits. It is difficult, from the fact that one is working in the dark, and requires a certain amount of dexterity, to be acquired only by practice. The instrument used is represented in Fig. 9. It is made by Messrs. Tiemann & Co., of New York. The operative procedure is as follows:

Fig. 9.

1. "The head of the rabbit is firmly held in the left hand. The operator feels with the finger of the right hand the tubercle situated in front of the ear, formed by the condyle of the lower jaw. Behind this tubercle, is a hard, osseous portion, the origin of the auditory canal.

2. "The operator penetrates just behind the superior border of the condyle, directing the point of the instrument slightly forward to avoid passing into the substance of the petrous portion of the temporal bone, and thus passes more easily into the middle temporal fossa; at the same time the instrument is directed a little upward to avoid slipping into the zygomatic fossa and thus failing to enter the cranial cavity.

3. "As soon as the instrument has penetrated the cranium, which is recognized by the point becoming free, the pressure is arrested and the instrument is directed downward and backward, its back sliding along the anterior face of the bone, which should serve as a guide in the operation.

4. "This point of departure—that is to say, the anterior face of the bone—being found, the instrument is pushed along, following its inferior border and proceeding gradually, as the instrument penetrates, pressing on the bone, the resistance of which can be easily recognized. Soon, how-

ever, the operator feels, at a certain depth, that the bony resistance ceases: he is then on the fifth pair, and the cries of the animal give evidence that the nerve is pressed upon.

5. "It is at this moment that it is necessary to hold firmly the instrument and the head of the animal; then the cutting edge is turned so as to be directed downward and backward, at the same time pressing in this direction so as to divide the nerve on the extremity of the petrous portion, behind the ganglion of Gasser, if possible, or at least on the ganglion itself.

6. "The instrument is then drawn back, pressing upon the bone so as to accomplish completely the section of the trunk of the fifth pair; then it is withdrawn by passing over the same course on the anterior face of the petrous portion so as not to lacerate the cerebral substance.

"The accident to be feared in the operation is section of the carotid when the instrument has penetrated too far, or lesion of the cavernous sinus when it is pressed too far forward."[1]

When this operation has been performed without accident, its immediate effects are very striking. The cornea and the integument and mucous membrane on that side of the head are instantaneously deprived of sensibility, and may be pricked, lacerated, or burned without the slightest evidence of pain on the part of the animal. Almost always the small root of the fifth is divided as well as the large root, and the muscles of mastication are paralyzed upon one side; but, with this exception, there is no paralysis of motion, sensation alone being destroyed upon one side.

Immediate Effects of Division of the Trifacial.—It is hardly necessary to discuss the functions of the trifacial, after the statement of the effects which instantly follow upon

[1] BERNARD, *Leçons sur la physiologie et la pathologie du système nerveux*, Paris, 1858, tome ii., p. 53.

its division, taken in connection with its physiological anatomy. The nerve has never been exposed in the cranial cavity in living animals; but its branches upon the face and the lingual branch of the inferior maxillary division have been operated upon and found to be exquisitely sensitive. Longet and others have exposed the roots in animals immediately after death, and have found that galvanization of the large root carefully insulated produces no muscular contraction.[1] All who have divided this root in living animals must have recognized, not only that it is sensitive, but that its sensibility is far more acute than that of any nervous trunk in the body. It is much more satisfactory to divide the nerve without etherizing the animal, as the evidence of pain is an important guide in this delicate operation; but in using anæsthetics, we have never been able to bring an animal under their influence so completely as to abolish the sensibility of the root itself. For example, in cats that appear to be thoroughly etherized, as soon as the instrument touches the nerve, there is more or less struggling. The large root of the fifth, then, is an exclusively sensory nerve, and its sensibility is more acute than that of any other of the cerebro-spinal nerves.

The distribution of the branches of the large root of the fifth indicates that it is the great sensitive nerve of the face. It will be remembered, however, that its branches go largely to the organs of special sense, and it is an interesting question to determine whether or not these branches be endowed with special as well as general sensibility.

Magendie thought, from his experiments upon animals, that the fifth nerve was endowed with special sensory properties. He states distinctly that section of the nerve is immediately followed by loss of taste, smell, hearing, and sight, on the side operated upon.[2] This view, however, has not

[1] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 487.

[2] MAGENDIE, *Suite des expériences sur les fonctions de la cinquième paire de nerfs.—Journal de physiologie*, Paris, 1824, tome iv., p. 305, *et seq.*

In another volume of the same journal, Magendie reports a case in which the

been sustained by more recent experimenters; and it is probable that in some of the experiments of Magendie, other nerves were divided as well as the fifth. This is a question which will be touched upon again in connection with the special senses; suffice it to say at present that there is no evidence that branches of the fifth pair of nerves are endowed with olfactory, auditory, or visual sensibility. This statement is made without reserve by Müller,[1] who adduces cases of paralysis of the fifth in the human subject in proof of its correctness. It is often the case that the special senses are affected as an indirect and remote consequence of lesion of the fifth, or rather of filaments of the sympathetic connected with the fifth; but division of this nerve alone does not immediately affect any of the special senses. The loss of taste is due always to division of the chorda tympani.

As far as audition and olfaction are concerned, there are no special effects immediately following section of the trifacial; but there are interesting phenomena observed in connection with the eye and the organs of taste.

At the instant of division of the fifth, by the method just described, the eyeball is protruded and the pupil becomes strongly contracted. This occurs in rabbits, and the contraction of the pupil was observed in the first operations of Magendie.[2] The pupil, however, is usually restored to the normal condition in a few hours. Longet states that the pupil is dilated by division of the fifth in dogs and cats.[3] After division of the nerve, the lachrymal secretion becomes very much less in quantity; but this is not the cause of the subsequent inflammation, for the eyes are not inflamed, as was shown by Magendie, even after extirpation of both lachrymal

sight in one eye was not extinct, the corresponding optic nerve being atrophied, but by no means destroyed (*La vue peut-elle être conservée malgré la destruction des nerfs optiques*, tome viii., p. 27).

[1] MÜLLER, *Physiologie du système nerveux*, Paris, 1840, tome i., p. 303.

[2] *Loc. cit.*

[3] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 489, note.

glands.[1] The movements of the eyeball are not affected by division of the fifth.

Another of the immediate effects of complete division of the fifth is loss of general sensibility in the tongue. This fact was noted by Mayo, in 1823,[2] and has been confirmed by other physiologists. Most experiments upon the influence of the fifth over the general sensibility and the sense of taste in the tongue have been made by dividing the lingual branch of the inferior maxillary division. When this branch is irritated, there are evidences of intense pain. When it is divided, the general sensibility and the sense of taste are destroyed in the anterior third or half of the tongue. It will be remembered, however, that the chorda tympani joins the lingual branch of the fifth as it passes between the pterygoid muscles, and that section of this branch of the facial abolishes the sense of taste in the anterior third or half of the tongue.[3] If the gustatory properties of the lingual branch of the fifth be derived from the chorda tympani, lesions of the fifth not involving this nerve would be followed by loss of general sensibility, but the taste would be unaffected. This has been shown to be the fact by experiments upon animals and certain cases of paralysis of general sensibility of the tongue without loss of taste in the human subject, reported by Schiff[4] and by Lussana,[5] which will be discussed more fully in connection with gustation.

Among the immediate effects of section of the fifth, is an interference with the reflex phenomena of deglutition. In some recent researches on the action of the sensitive nerves

[1] MAGENDIE, *De l'influence de la cinquième paire des nerfs sur la nutrition et les fonctions de l'œil.—Journal de physiologie*, Paris, 1824, tome iv., p. 179.

[2] MAYO, *Anatomical and Physiological Commentaries*, Number ii., London, 1823, p. 10.

[3] See page 155, *et seq.*

[4] SCHIFF, *Leçons sur la physiologie de la digestion*, Florence et Turin, 1867, tome i., p. 103, *et seq.*

[5] LUSSANA, *Recherches expérimentales et observations pathologiques sur les nerfs du gout.—Archives de physiologie*, Paris, 1869, tome ii., p. 27, *et seq.*

in deglutition, by Waller and Prevost, it was found, that after section of the fifth upon both sides, it was impossible to excite movements of deglutition by stimulating the mucous membrane of the velum palati. After section of the superior laryngeal branches of the pneumogastrics, no movements of deglutition followed stimulation of the mucous membrane of the top of the larynx. In these experiments, when the fifth was divided on one side, stimulation of the velum upon the corresponding side had no effect, while movements of deglutition were produced by irritating the velum upon the sound side.[1] These experiments show that the fifth nerve is important in the reflex phenomena of deglutition, as a sensory nerve, conveying the impression from the velum palati to the nerve-centres. This action probably takes place through filaments which pass from the fifth to the mucous membrane through Meckel's ganglion.

Remote Effects of Division of the Trifacial.—After the ordinary operation of dividing the fifth pair in the cranial cavity, the immediate loss of sensibility of the integument and mucous membranes of the face and head is usually supplemented by serious disturbances in the nutrition of the eye, the ear, and the mucous membranes of the nose and mouth. This curious fact was noted by Magendie, in 1824;[2] but it was observed by Mayo, in 1823, in a case of paralysis of the fifth in the human subject.[3] At a period varying from a few hours to one or two days after the operation, the eye upon the affected side becomes the seat of purulent inflammation, the cornea becomes opaque, ulcerates, the humors are discharged, and the organ is destroyed. Congestion of the parts is usually very prominent a few hours after

[1] Waller et Prevost, *Étude relative aux nerfs sensitifs qui président aux phénomènes reflexes de la deglutition.—Archives de physiologie*, Paris, 1870, tome iii., p. 346, *et seq.*

[2] *Journal de physiologie*, Paris, 1824, tome iv., pp. 178, 304.

[3] Mayo, *Anatomical and Physiological Commentaries*, Number ii., London, 1823, p. 12.

division of the nerve. At the same time, there is an increased discharge from the mucous membranes of the nose and mouth upon the affected side, and ulcers appear upon the tongue and lips. It is probable, also, that disorders in the nutrition of the auditory apparatus follow the operation, though these are not so prominent. These phenomena undoubtedly led Magendie to advance the view that section of the fifth involves destruction of the organs of special sense,[1] though, as we have seen, these results are consecutive and not immediate. Animals affected in this way usually die in from fifteen to twenty days.

One of the most interesting facts, particularly in view of the information derived from later observations, in connection with the early experiments of Magendie, is, that he noted that "the alterations in nutrition are much less marked"[2] when the division is effected behind the ganglion of Gasser, than when it is done in the ordinary way through the ganglion. It is difficult enough to divide the nerve completely within the cranium, and is almost impossible to make the operation at will through or behind the ganglion, and the phenomena of inflammation are absent only in exceptional and accidental instances. Magendie offers no satisfactory explanation of the differences in the consecutive phenomena coincident with the locality of section of the nerve. The facts, however, have been abundantly verified by Longet,[3] Bernard,[4] and other experimenters. In the numerous experiments that we have made upon the fifth pair, we have generally noted the consecutive inflammatory phenomena in the order above described; but in exceptional instances, these phenomena have been wanting. The following experiment illustrates these exceptional operations:

[1] *Loc. cit.* [2] *Journal de physiologie*, Paris, 1824, tome iv., p. 304.

[3] LONGET, *Anatomie et physiologie du système nerveux*, Paris, 1842, tome ii., p. 162.

[4] BERNARD, *Leçons sur la physiologie et la pathologie du système nerveux*, Paris, 1858, tome ii., p. 60.

February 6, 1868, the fifth pair of nerves was divided upon the left side in a full-grown rabbit in the ordinary way, before the class at the Bellevue Hospital Medical College. There followed instant and complete loss of sensibility on the left side of the face. Four days after, the animal having been fed *ad libitum* with cabbage, the loss of sensibility was still complete. There was very little redness of the conjunctiva of the left eye, and a very slight streak of opacity, so slight that it was distinguished with difficulty. Twelve days after the operation, the sensibility of the left eye was distinct, but slight.[1] There was no redness of the conjunctiva, and the opacity of the cornea had disappeared. The animal was in good condition, the line of contact of the upper with the lower incisors, when the jaws were closed, was very oblique. The animal was kept alive by careful feeding with bread and milk for one hundred and seven days after the operation, there never being any inflammation of the organs of special sense. It died at that time of inanition, having become very much emaciated. The animal never recovered power over the muscles of mastication of the left side, and the incisors grew to a great length, interfering very much with mastication, which seemed to be the cause of death.

Longet, in 1842, furnished a satisfactory explanation of the absence of inflammation in certain cases of division of the fifth. He attributed the consecutive inflammation in most experiments to lesion of the ganglion of Gasser and of the sympathetic connections, which are very numerous at this point. These sympathetic filaments are avoided when the section is made behind the ganglion.[2]

The explanation of the phenomena of disordered nutrition in the organs of special sense, particularly the eye, following division of the fifth, is not afforded by the section of this nerve alone; for, as we have seen, when the loss of sen-

[1] We have observed in other experiments gradual return of sensibility, after what appeared to have been complete division of the fifth.

[2] Longet, *Anatomie et physiologie du système nerveux*, Paris, 1842, tome ii., p. 162.

sibility is complete after division of the nerve behind the Gasserian ganglion, these results may not follow. Nor are they explained by deficiency in the lachrymal secretion, for they are not observed when both lachrymal glands have been extirpated. They are not due to exposure of the eye-ball, for they do not follow upon section of the facial. Nor are they due simply to an enfeebled general condition, for, in the experiment we have detailed, the animal died of inanition after section of the nerve, without any evidences of inflammation. In view of the fact that section of sympathetic filaments is well known to modify the nutrition of parts to which they are distributed, producing congestion, increase in temperature, and other phenomena, it is rational to infer that the modifications in nutrition which follow section of the fifth after it receives filaments from the sympathetic system, not occurring when these sympathetic filaments escape division, are to be attributed to lesion of the sympathetic, and not the division of the sensory nerve itself.

A farther explanation is demanded for the inflammatory results which follow division of the sympathetic filaments joining the fifth, inasmuch as division of the sympathetic alone in the neck produces simply exaggeration of the nutritive processes, as evidenced chiefly by local increase in the animal temperature, and not the well-known phenomena of inflammation.

It has been remarked by Bernard, that the "alterations in nutrition appear more promptly in animals that are enfeebled."[1] Section of the small root of the fifth, which is unavoidable when the nerve is divided in the cranial cavity, generally interferes so much with mastication as to influence seriously the general nutrition; and this might modify the

[1] BERNARD, *Leçons sur la physiologie et la pathologie du système nerveux*, Paris, 1858, tome ii., p. 62. Bernard (*op. cit.*, p. 518), in discussing the effects upon calorification and nutrition of the face of division of the sympathetic in the neck, states that "the effects of calorification of the great sympathetic may be transformed into inflammatory phenomena when the animal becomes enfeebled." He divided the sympathetic with the pneumogastric in the neck of a dog, on the

nutritive processes in delicate organs, like the eye, so as to induce those changes which are called inflammatory. The following observation, communicated by Dr. W. H. Mason, Professor of Physiology in the Medical Department of the University of Buffalo, is very striking in this connection:

The fifth pair of nerves was divided in a cat in the ordinary way. By feeding the animal carefully with milk and finely-chopped meat, the nutrition was maintained at a high standard, and no inflammation of the eye occurred for about four weeks. The supply of food was then diminished to about the quantity it would be able to take without any special care, when the eye became inflamed, and perforation of the cornea and destruction of the organ followed. The animal was kept for about five months; at the end of which time, sensation on the affected side, which had been gradually improving, was completely restored.[1]

The explanation we have to offer of the consecutive inflammatory effects of section of the fifth with its communicating sympathetic filaments is the following: By dividing the sympathetic, the eye and the mucous membranes of the nose, mouth, and ear are rendered hyperæmic, the temperature is probably raised, and the processes of nutrition are exaggerated. This condition of the parts would seem to require a full supply of nutritive material from the blood, in order to maintain the condition of exaggerated nutrition; but when the blood is impoverished, probably as the result of deficiency in the introduction of nutritive matter, from paraly-

left side. A few days after, he made experiments on the salivary secretion, and finally took away a portion of the cephalo-rachidian fluid. "This last operation made the animal sick and produced an inflammation of the nervous centres: death occurred five days after. What was remarkable was that the mucous membranes on the side of the face corresponding to the section of the sympathetic became the seat of violent inflammation, from the moment that the animal began to become enfeebled from the disease. There was abundant suppuration from the nostril, the buccal mucous membrane, and the conjunctiva of the left side, while on the opposite side the corresponding mucous membranes were in the normal condition."

[1] Written communication from Prof. Mason.

sis of the muscles of mastication upon one side, the nutritive processes in these delicate parts are seriously modified, so as to constitute inflammation. The observation just detailed is an argument in favor of this view; for here the inflammatory action seemed to be arrested when the action of the paralyzed muscles was supplied by careful feeding. With this view, the disorders of nutrition observed after division of the fifth may properly be referred to the sympathetic system.

Pathological facts in confirmation of experiments upon the fifth pair in the lower animals are not wanting; but it must be remembered that, in cases of paralysis of the nerve in the human subject, it is not always possible to locate exactly the seat of the lesion and to appreciate fully its extent, as can be done when the nerve is divided by an operation. In studying these cases, it sometimes occurs that the phenomena, particularly those of modified nutrition, are more or less contradictory.

In nearly all the works on physiology, we find references to cases of paralysis of the fifth in the human subject. One of the most interesting is the case already referred to, reported by Mayo, which was published before the experiments of Magendie.[1] Numerous cases of this kind have been collected by Longet.[2] In the appendix to the work of Sir Charles Bell on the Nervous System, several cases are reported,[3] observed by himself and collated from various sources. We have already referred to the cases cited by Schiff and by Lussana, some of which showed alteration of taste, while in others this symptom was absent.[4] In a recent article by Dr. H. D. Noyes, Professor of Ophthalmology in the Bellevue Hospital Medical College, two interest-

[1] See page 196.

[2] LONGET, *Anatomie et physiologie du système nerveux*, Paris, 1842, tome ii., p. 191, *et seq.*

[3] BELL, *The Nervous System of the Human Body*, London, 1844, Appendix.

[4] See page 195.

It is unnecessary to cite all the cases reported of paralysis of the fifth, but they are quite numerous. In addition to those already referred to, the following

ing cases are reported, which we had an opportunity of examining during the progress of treatment. In both of these cases, there was inflammation of the eye. In one case, the tongue was entirely insensible upon on side, but there was no impairment of the sense of taste. An interesting feature in one of the cases was the fact that an operation upon the eyelid of the affected side was performed without the slightest evidence of pain on the part of the patient.[1]

These cases of paralysis of the fifth in the human subject in the main confirm the results of experiments upon the inferior animals. In all the cases in which the fifth nerve alone was involved in the disease, without the portio dura of the seventh, there was simply loss of sensibility upon one side, the movements of the superficial muscles of the face being unaffected. When the small root was involved, the muscles of mastication upon one side were paralyzed; but in certain cases in which this root escaped, there was no muscular paralysis. The sense of sight, hearing, and smell, except as they were affected by consecutive inflammation, were little, if at all, disturbed in uncomplicated cases. The sense of taste in the anterior portion of the tongue was perfect, except in those cases in which the seventh, the chorda tympani, or the lingual branch of the fifth after it had been joined by the chorda tympani, was involved in the disease. In some cases, there was no alteration in the nutrition of the organs of special sense; but in this respect the facts with regard to the seat of the lesion are not so satisfactory as in experiments upon the lower animals, it being difficult, in most of them, to limit the exact boundaries of the lesion.

are the most important and satisfactory in their details: The case reported by Montault (*Journal de physiologie*, Paris, 1829, tome ix., p. 113); a case by Dr. Beveridge (*Medical Times and Gazette*, London, 1868, No. 921, p. 199); a case by Althaus (*Medico-Chirurgical Transactions*, London, 1869, vol. lii., p. 27); and two cases by Rosenthal (*Medicinische Jahrbücher*, Wien, 1870, Bd. xix., Heft ii. und iii., S. 163).

[1] NOYES, *Paralysis of the Fifth Cerebral Nerve, and its Effects.—New York Medical Journal*, 1871, vol. xiv., p. 163, *et seq.*

CHAPTER VIII.

PNEUMOGASTRIC, OR PAR VAGUM NERVE.

Pneumogastric nerve (second division of the eighth)—Physiological anatomy—Properties and functions of the pneumogastric—General properties of the roots—Properties and functions of the auricular nerves—Properties and functions of the pharyngeal nerves—Properties and functions of the superior laryngeal nerves—Properties and functions of the inferior, or recurrent laryngeal nerves—Properties and functions of the cardiac nerves, and influence of the pneumogastrics upon the circulation—Depressor-nerve of the circulation—Properties and functions of the pulmonary branches, and influence of the pneumogastrics upon respiration—Properties and functions of the œsophageal nerves—Properties and functions of the abdominal branches—Influence of the pneumogastrics upon the liver—Influence of the pneumogastrics upon the stomach and intestines—Summary of the distribution, properties, and functions, of the pneumogastrics.

Of all the nerves emerging from the cranial cavity, the pneumogastric, the second division of the eighth pair, presents the greatest number of anastomoses, the most remarkable course, and the most varied and interesting functions. Arising from the medulla oblongata by a purely sensory root, it communicates with at least five motor nerves in its course, and is distributed largely to muscular tissue, both of the voluntary and the involuntary variety. Finally, there is no nerve that has been the subject of such extended and elaborate anatomical and physiological investigations, and none, concerning the properties and exact functions of which there has been so much difference of opinion.

We shall have to treat of the influence of the pneumogastric upon the act of deglutition, the heart and circulatory

system, the respiratory system, the stomach, intestines, and various glandular organs. An indispensable introduction to this study is a description of its physiological anatomy.

Physiological Anatomy.—The apparent origin of the pneumogastric is from the lateral portion of the medulla oblongata, just behind the olivary body, between the roots of the glosso-pharyngeal and of the spinal accessory. The deep origin is mainly from what is sometimes called the nucleus of the pneumogastric, in the inferior portion of the gray substance in the floor of the fourth ventricle. The course of the fibres, traced from without inward, is somewhat intricate. The description of these, given by Vulpian, in 1853, has been pretty generally verified by more recent dissections, as well as by microscopical investigations.

Vulpian regards the deep origins of the pneumogastric and glosso-pharyngeal nerves as, in the main, identical. Tracing the filaments from without inward, he was able to follow them in four directions. The anterior filaments pass from without inward, first very superficial and directed toward the olivary body, but turning before they reach the olivary body, they pass deeply into the substance of the restiform body, in which they are lost. The posterior filaments are superficial, and pass, with the fibres of the restiform body, toward the cerebellum. Of the intermediate filaments, the anterior pass through the restiform body, the greatest number extending to the median line in the floor of the fourth ventricle. A few fibres are lost in the middle fasciculi of the medulla, and a few pass toward the brain. The posterior intermediate filaments traverse the restiform body to the floor of the fourth ventricle, when some pass to the median line, and others descend in the substance of the medulla.[1] Vulpian states that he has not been able to follow the fibres of origin of the pneumogastrics beyond the

[1] VULPIAN, *Essai sur l'origine de plusieurs paires des nerfs craniens, Thèse*, Paris, 1853, p. 39.

median line, but more recent observations leave no doubt of the fact that many of these fibres decussate in the floor of the fourth ventricle.[1]

There are two ganglionic enlargements belonging to the pneumogastric. In the jugular foramen, is a well-marked, grayish, ovoid enlargement, from one-sixth to one-fourth of an inch in length, called the jugular ganglion, or the ganglion of the root. This is united by two or three filaments with the ganglion of the glosso-pharyngeal. It is a true ganglion, containing nerve-cells. After the nerve has emerged from the cranial cavity, it presents on its trunk another grayish enlargement, from half an inch to an inch in length, called the ganglion of the trunk. This is of rather a plexiform structure, the white fibres being mixed with grayish fibres and nerve-cells.

The exit of the nerve from the cranial cavity is by the jugular foramen, or posterior foramen lacerum, in company with the spinal accessory, the glosso-pharyngeal, and the internal jugular vein.

Anastomoses.—The filaments of communication which the pneumogastric receives from other nerves are interesting from their great importance and their varied sources. The most important of these is the branch from the spinal accessory. There are occasional filaments of communication which pass from the spinal accessory to the ganglion of the root, but they are not constant. After both nerves have emerged from the cranial cavity, an important branch of considerable size passes from the spinal accessory to the pneumogastric, with which it becomes closely united. Experiments have shown that these filaments from the spinal accessory pass in great part to the larynx by the inferior laryngeal nerves.

In the aquæductus Fallopii, the facial nerve gives off a

[1] DEAN, *The Gray Substance of the Medulla Oblongata and Trapezium*, Washington, 1864, p. 27.

filament of communication to the pneumogastric at the ganglion of the root. This filament, joined at the ganglion by sensory filaments from the pneumogastric and some filaments from the glosso-pharyngeal, is called the auricular branch of Arnold. By some anatomists, it is regarded as a branch from the facial,[1] and by others it is described with the pneumogastric.[2]

Two or three small filaments of communication pass from the sublingual to the ganglion of the trunk of the pneumogastric.

At the ganglion of the trunk, the pneumogastric generally receives filaments of communication from the arcade formed by the anterior branches of the first two cervical nerves. These, however, are not constant.

The pneumogastric is connected with the sympathetic system by numerous delicate filaments of communication received from the superior cervical ganglion, passing in part upward toward the ganglion of the root of the pneumogastric, and in part transversely and downward. These filaments are frequently short, and, as it were, bind the sympathetic ganglion to the trunk of the nerve. The main trunk of the pneumogastric and its branches receive a few delicate filaments of communication from the middle and inferior cervical and the upper dorsal ganglia of the sympathetic.

The pneumogastric frequently sends a very delicate filament to the glosso-pharyngeal nerve, at or near the ganglion of Andersch. Branches from the pneumogastric join branches from the glosso-pharyngeal, the spinal accessory, and the sympathetic, to form the pharyngeal plexus.

Distribution.—In describing the very extensive distribution of the pneumogastrics, while the nerves upon the two sides do not present any important differences in the destination of their filaments as far down as the diaphragm, it

[1] HIRSCHFELD, *Système nerveux*, Paris, 1866, p. 205.

[2] SAPPEY, *Traité d'anatomie*, Paris, 1852, tome ii., p. 287.

will be seen that the abdominal branches are not the same. The most important branches are the following:

1. Auricular.
2. Pharyngeal.
3. Superior laryngeal.
4. Inferior, or recurrent laryngeal.
5. Cardiac, cervical and thoracic.
6. Pulmonary, anterior and posterior.
7. Œsophageal.
8. Abdominal.

The auricular nerves are sometimes described in connection with the facial. They are given off from the ganglion of the trunk, and are composed of filaments of communication from the facial and from the glosso-pharyngeal, as well as of filaments from the pneumogastric itself. The nerve thus constituted is distributed to the integument of the upper portion of the external auditory meatus, and a small filament, according to Sappey, is sent to the membrana tympani.[1]

The pharyngeal nerves are very remarkable in their course. They are given off from the superior portion of the ganglion of the trunk, and contain a large number of the filaments of communication which the pneumogastric receives from the spinal accessory. In their course by the sides of the superior constrictor muscles of the pharynx, these nerves anastomose with numerous filaments from the glosso-pharyngeal and the superior cervical ganglion of the sympathetic, to form what is known as the pharyngeal plexus. The ultimate filaments of distribution pass to the muscles and the mucous membrane of the pharynx. Physiological experiments have shown that the motor influence transmitted to the pharyngeal muscles through the pharyngeal branches of the pneumogastric is derived from the spinal accessory.[2]

The superior laryngeal nerves are given off from the

[1] SAPPEY, *Traité d'anatomie*, Paris, 1852, tome ii., p. 287. [2] See page 175.

lower part of the ganglion of the trunk. Their filaments come from the side opposite to the point of junction of the pneumogastric with the communicating branch from the spinal accessory, so that probably the superior laryngeals contain few if any motor fibres from this nerve. The superior laryngeal gives off the external laryngeal, a long, delicate branch, which gives a few filaments to the inferior constrictor of the pharynx, and is distributed to the crico-thyroid muscle and the mucous membrane of the ventricle of the larynx. The external laryngeal anastomoses with the inferior laryngeal and with the sympathetic. The internal branch is distributed to the mucous membrane of the epiglottis, the base of the tongue, the aryteno-epiglottidean fold, and the mucous membrane of the larynx as far down as the true vocal cords. A branch from this nerve, in its course to the larynx, penetrates the arytenoid muscle, to which it sends a few filaments, but these are all sensory. This branch also supplies the crico-thyroid muscle. It anastomoses with the inferior laryngeal nerve. An important branch, described by Cyon and Ludwig, in the rabbit, under the name of the depressor-nerve, arises by two roots, one from the superior laryngeal and another from the trunk of the pneumogastric, passes down the neck by the side of the sympathetic, and, in the chest, joins filaments from the thoracic sympathetic, to penetrate the heart between the aorta and the pulmonary artery.[1] This nerve will be referred to more particularly in connection with the influence of the pneumogastrics upon the circulation.

It is important, from a physiological point of view, to note that the superior laryngeal nerve is the nerve of sensibility of the upper part of the larynx, as well as the supralaryngeal mucous membranes, and that it animates a single muscle of the larynx, the crico-thyroid, and the inferior constrictor of the pharynx.

[1] Cyon et Ludwig, *Action réflexe d'un des nerfs sensibles du cœur sur les nerfs vaso-moteurs.—Journal de l'anatomie*, Paris, 1867, tome iv., p. 472, *et seq.*

The inferior, or recurrent laryngeal nerves present some slight differences in their anatomy upon the two sides. Upon the left side, the nerve is the larger, and is given off at the arch of the aorta. Passing beneath this vessel, it ascends in the groove between the trachea and the œsophagus. In its upward course, it gives off certain filaments which join the cardiac branches, filaments to the muscular tissue and mucous membrane of the upper part of the œsophagus, filaments to the mucous membrane and the inter-cartilaginous muscular tissue of the trachea, one or two filaments to the inferior constrictor of the pharynx, and a branch which joins the superior laryngeal. Its terminal branches penetrate the larynx behind the posterior articulation of the thyroid with the cricoid cartilage, and are distributed to all of the intrinsic muscles of the larynx, except the crico-thyroids, which are supplied by the superior laryngeal.

Upon the right side, the nerve winds from before backward around the subclavian artery, and has essentially the same course and distribution as upon the left side, except that it is smaller and its filaments of distribution are not so numerous.

The important physiological point connected with the anatomy of the recurrent laryngeals is that they animate all of the intrinsic muscles of the larynx, except the crico-thyroid. Experiments have shown that these nerves contain numerous filaments from the spinal accessory.

The cervical cardiac branches, two or three in number, arise from the pneumogastrics at different points of the cervical portion and pass to the cardiac plexus, which is formed in great part of filaments from the sympathetic. The thoracic cardiac branches are given off from the pneumogastrics below the origin of the inferior laryngeals, and join the cardiac plexus.

The anterior pulmonary branches are few and delicate as compared with the posterior branches. They are given off below the origin of the thoracic cardiac branches, send

a few filaments to the trachea, then form a plexus which surrounds the bronchial tubes and follows the bronchial tree to its terminations in the air-cells. The posterior pulmonary branches are larger and more numerous than the anterior. They communicate freely with sympathetic filaments from the upper three or four thoracic ganglia, and then form the great posterior pulmonary plexus. From this plexus, a few filaments go to the inferior and posterior portion of the trachea; a few pass to the muscular tissue and mucous membrane of the middle portion of the œsophagus; and a few are sent to the posterior and superior portion of the pericardium. The plexus then surrounds the bronchial tree, and passes with its ramifications to the pulmonary tissue, like the corresponding filaments of the anterior branches. According to Sappey, the pulmonary branches are distributed to the mucous membrane, and not to the walls of the blood-vessels.[1]

The œsophageal branches take their origin from the pneumogastrics above and below the pulmonary branches. These branches from the two sides join to form the œsophageal plexus, their filaments of distribution going to the muscular tissue and the mucous membrane of the lower third of the œsophagus.

The abdominal branches are quite different in their distribution upon the two sides.

On the left side, the nerve, which is situated anterior to the cardiac opening of the stomach, immediately after its passage by the side of the œsophagus into the abdomen, divides into numerous branches, which are distributed to the muscular walls and the mucous membrane of the stomach. As the branches pass from the lesser curvature, they take a downward direction and go to the liver, and, with another branch running between the folds of the gastro-hepatic omentum, follow the course of the portal vein in the hepatic substance. The branches of this nerve anastomose with the nerve on the right side and with the sympathetic.

[1] SAPPEY, *Traité d'anatomie*, Paris, 1852, tome ii., p. 294.

The right pneumogastric, situated posteriorly, at the œsophageal opening of the diaphragm, sends a few filaments to the muscular coat and the mucous membrane of the stomach, passes backward, and is distributed to the liver, spleen, kidneys, suprarenal capsules, and finally to the whole of the small intestine.

The branches to the small intestine are very important. These were accurately described in 1860, by Kollmann, in an elaborate and beautifully-illustrated prize-essay. In the plate showing the distribution of this nerve, it is seen that the branches to the intestine are very numerous. According to these researches, the branches described belong to the pneumogastric itself, and are not derived from the sympathetic.[1] When we come to treat of the action of the pneumogastric upon the small intestine, it will be seen that the anatomical researches by Kollmann are fully confirmed by physiological experiments. Before the nerves pass to the intestines, there is a free anastomosis and interchange of filaments between the right and the left pneumogastric.

Properties and Functions of the Pneumogastric Nerves.

There is no nerve in the body that has been the subject of so many experiments, and concerning which so much has been written, as the pneumogastric. Its accessible position in many parts of its course, its extensive connections with the digestive, the respiratory, and the circulatory system, and the evident importance of its relations, have rendered the literature connected with its physiology somewhat redundant. We do not propose to discuss in full all of the views entertained from time to time with regard to its functions, but to state merely what seem to be well-ascertained facts, and the most reasonable inferences, where the facts are diffi-

[1] KOLLMANN, *Ueber den Verlauf des Lungenmagennerven in der Bauchhöle. Eine Preisschrift.—Zeitschrift für wissenschaftliche Zoologie*, Leipzig, 1860, Bd. x., S. 413, *et seq.*

cult of demonstration. In treating of the functions of this nerve, we shall be compelled to make constant reference to its anatomy, and for that reason have described pretty fully in detail most of the important points in its connections and distribution.

Although the extensive distribution of the pneumogastrics and their importance will necessitate a long discussion of their physiology, we shall endeavor to separate the points to be considered distinctly, and simplify the subject as much as possible.

We shall first treat of the general properties of those filaments derived from the true roots of the nerves, and, following them in their course, shall note the properties derived from their connections with other nerves.

We shall then treat of the properties of the different branches of the nerves, under distinct heads, taking up these branches as they are given off, from above downward. In this, we shall consider first the properties and functions of the auricular branches; next, of the pharyngeal branches, with their influence upon the action of the pharynx in deglutition; next, the superior and inferior laryngeal branches, with their relations to the physiology of the larynx; next the cardiac branches, with their influence on the movements of the heart and the circulation; next, the pulmonary branches, with the function of the nerves in connection with respiration; next, the œsophageal branches, in connection with the influence of the nerves upon the action of the œsophagus, in deglutition; next, the abdominal branches, with the influence of the nerves in connection with digestion and the functions of the abdominal viscera. By dividing up, in this way, the action of the pneumogastrics, it is hoped that their physiology may be relieved of much of the complexity in which it is apparently involved.

General Properties of the Roots of Origin of the Pneumogastrics.—All who have operated on the pneumogastrics

in the cervical region in living animals have noted their exceedingly dull sensibility, as compared with the ordinary sensory nerves. Bernard, indeed, states that in this region they are generally insensible;[1] but we have usually found, in dogs at least, that their division is attended with slight evidences of pain. Without citing in detail all the experiments on this point, it is sufficient to state that some physiologists, on galvanizing or otherwise irritating the roots of the nerves in animals just killed, have noted movements of the muscles of deglutition, of the œsophagus, and the muscular coats of the stomach. These experiments have led to the opinion that the proper roots of the nerves are motor as well as sensory. It becomes, therefore, a difficult as well as an important point to determine whether or not the roots be of themselves exclusively sensory or mixed.

In discussing the properties of the roots, we shall rely almost entirely upon direct experiments; though the arguments drawn from their anatomical characters, in the presence of ganglia and the deep origin of their fibres, point strongly to their sensory character.

It is impossible to stimulate the roots, before they have received motor filaments from other nerves, in living animals, and the experiments are therefore made upon animals just killed, before the nervous irritability has disappeared. If the true roots of the nerves be exclusively sensory, their galvanization in animals just killed should produce, by direct action, no muscular contraction. If the roots contain any motor filaments, contraction of muscles should follow their stimulation. The proper physiological conditions in such experiments are the following:

1. It is necessary to stimulate the roots so that the filaments from the spinal accessory and other motor nerves be not involved.

2. It is important to ascertain, provided movements follow such irritation, whether or not they be due to reflex action.

[1] Bernard, *Système nerveux*, Paris, 1858, tome ii., p. 345.

The first of these conditions is easily fulfilled. All that is necessary is to stimulate the roots before the nerves have received any anastomosing filaments. To avoid contractions of muscles due to reflex action, it is best to divide the roots and to stimulate their distal portion. If it be true that stimulation of the distal extremities of the roots, the irritation so applied as not to involve communicating filaments from motor nerves, and not to be conveyed to the centres, producing reflex movements through other nerves, does not produce any movements, it is fair to assume that the true filaments of origin are exclusively sensory. The facts upon this point demand careful and critical study; and it will be proper to discard the earlier experiments, made before the mechanism of reflex action had been satisfactorily established.

If the experiments of Longet be accepted without reserve, they prove—as conclusively as is possible without exposing the roots in living animals, an operation which is impracticable—that the true filaments of origin of the pneumogastrics are exclusively sensory; at least, that the nerve contains no motor filaments except those derived from other nerves. The following quotation gives the essential points in these experiments:

"In dogs of large size and in horses, I have isolated in the cranium, with the most minute care, the pneumogastric of the medulla oblongata and the superior filaments of the spinal accessory (*internal branch*), in order to avoid all *reflex movement* and any derivative current upon the last-named nerve; I then immediately caused the current to act exclusively upon the filaments of origin of the pneumogastric, without having ever seen the slightest contraction supervene, either in the muscles of the larynx or pharynx, or in the muscular tunic of the œsophagus, or elsewhere.

"But also I have never failed to demonstrate to all those who witnessed my experiments, how it is easy to obtain opposite results in neglecting only one precaution: it suffices,

for example, to slightly moisten the slip of glass or oiled silk which serves to isolate the two nerves, in order that the current should act immediately upon the superior filaments of the spinal accessory, from which we have marked contractions in the organs just mentioned." [1]

These experiments seem entirely conclusive. In treating of the reflex phenomena of deglutition and their relations to the superior branches of the pneumogastric, the pharyngeal, and the superior laryngeal, it will be seen that irritation, either of these nerves or of the mucous membranes to which they are distributed, will produce contractions in the muscles. All who are practically familiar with the application of electricity to the nerves know how difficult it is to insulate the nervous trunks so as to avoid the influence of "derived" currents. In carefully studying the experiments of Longet, it seems that all the physiological conditions were fulfilled; and that when the nerve is divided at the root and the stimulation is applied to the peripheral end, so as to cut off all reflex action from the nervous centres, and when sufficient care is exercised to prevent the propagation of the current to the motor connections of the pneumogastric, the nerve, from its origin at the medulla oblongata to the ganglion of the root, contains no motor filaments, and is therefore exclusively sensory.

Among the more recent experiments which have led to the view that the roots of the pneumogastrics contain motor filaments, are those of Chauveau, made in 1862, and of Van Kempen, published in 1863. In the experiments of Chauveau, the excitation was applied to the roots of the nerves in animals just killed, with the effect of producing energetic contractions of the œsophagus and stomach. The roots, however, were not divided.[2] It is stated in this article that all reflex action ceases in adult mammals with the move-

[1] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 508.

[2] CHAUVEAU, *Du nerf pneumogastrique, etc.—Journal de la physiologie*, Paris, 1862, tome v., p. 198.

ments of the heart.[1] This assumption is too broad; and certainly it would not have been less accurate, and would have answered a vital objection, if the nerve had been divided and galvanization had been applied to its peripheral extremity; for it is well known that so long as the motor nerves and the muscles retain their irritability, contractions will follow their stimulation after they have been separated from the centres. In the experiments just cited, there is every reason to believe that the contractions of the œsophagus and stomach were purely reflex. The remarks just made concerning the experiments of Chauveau are equally applicable to those of Van Kempen, in which it is not stated that the roots were divided;[2] and, as far as we know, there are no direct observations showing contraction of muscular tissue following stimulation of the roots of the pneumogastrics, which cannot be explained by the principle of reflex action, or by the supposition that the stimulation was extended to communicating motor filaments. In view of these facts, we do not consider it necessary to discuss the question more fully in detail, and will adopt, without reserve, the conclusions of Longet, that the true filaments of origin of the pneumogastrics are exclusively sensory, or, at least, that they have no motor properties.

Properties and Functions of the Auricular Nerves.—There is very little to be said with regard to the auricular nerves, after the description we have given of their anatomy. They are sometimes described with the facial and sometimes with the pneumogastric. They contain filaments from the facial, the pneumogastric, and the glosso-pharyngeal. The sensory filaments of these nerves give sensibility to the upper part of the external auditory meatus and the membrana tympani.

[1] CHAUVEAU, *Du nerf pneumogastrique, etc.—Journal de la physiologie*, Paris, 1862, tome v., p. 193.

[2] VAN KEMPEN, *Nouvelles recherches sur la nature fonctionelle des racines du nerf pneumogastrique et du nerf spinal.—Journal de la physiologie*, Paris, 1863, tome vi., p. 284, *et seq.*

Properties and Functions of the Pharyngeal Nerves.—The pharyngeal branches of the pneumogastric are mixed nerves, their motor filaments being derived from the spinal accessory. Their direct action upon the muscles of deglutition belongs to the physiological history of the last-named nerve. We have already stated, in treating of the spinal accessory, that the filaments of communication that go to the pharyngeal branches of the pneumogastric are distributed to the pharyngeal muscles.[1]

It is impossible to divide all of the pharyngeal filaments in living animals and observe directly how far the general sensibility of the pharynx and the reflex phenomena of deglutition are influenced by this section. As far as we can judge from the distribution of the filaments to the mucous membrane, it would seem that they combine with the pharyngeal filaments of the fifth, and possibly sensory filaments from the glosso-pharyngeal, in giving general sensibility to these parts.

In some recent experiments by Waller and Prevost, on the reflex phenomena of deglutition, it is shown that the action of the pharyngeal muscles cannot be excited by stimulation of the mucous membrane of the supralaryngeal region and the pharynx, after section of the fifth and the superior laryngeal branch of the pneumogastrics.[2] This would seem to show that the pharyngeal branches of the pneumogastrics are of little or no importance in these reflex phenomena.

Properties and Functions of the Superior Laryngeal Nerves.—The distribution of these nerves points to a double function; viz., an action upon the crico-thyroid muscles, and the important office of supplying general sensibility to the upper part of the larynx and a portion of the surrounding mucous membrane.

[1] See page 175.

[2] Waller et Prevost, *Étude relative aux nerfs sensitifs qui président aux phénomènes réflexes de la déglutition.—Archives de physiologie*, Paris, 1870, tome iii., p. 347.

The stimulation of these nerves produces intense pain and contraction of the crico-thyroids; but it has been shown by experiment that the arytenoid muscles, through which the nerves pass, receive no motor filaments.[1]

The action of the nerves upon the muscles is very simple, and resolves itself into the function of the crico-thyroids, which has been treated of fully under the head of phonation.[2] When these muscles are paralyzed, the voice becomes hoarse. The filaments to the inferior muscles of the pharynx are few and comparatively unimportant. It is important in this connection to note that the superior laryngeals do not receive their motor filaments from the spinal accessory.

The sensory filaments of the superior laryngeals have important functions connected with the protection of the air-passages from the entrance of foreign matters, particularly in deglutition, and are further concerned, as we shall see, in the reflex action of the constrictors of the pharynx. In treating of deglutition, in another volume, we have fully discussed the importance of the exquisite sensibility of the top of the larynx in the protection of the air-passages. When both superior laryngeals have been divided in living animals, liquids often pass into the larynx in small quantity, owing to the absence of the reflex closure of the glottis when foreign matters are brought in contact with its superior surface, and the occasional occurrence of inspiration during deglutition.[3]

Aside from the protection of the air-passages, the superior laryngeal is one of the sensory nerves through which the reflex acts in deglutition operate. There are certain parts which depend for their sensibility entirely upon this nerve; viz., the mucous membrane of the epiglottis, the aryteno-epiglottidean fold, and the larynx, as far down as the true vocal cords. When an impression is made upon these parts, as

[1] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 525.

[2] See vol. iii., Voice and Speech, p. 495. [3] See vol. ii., Digestion, p. 197.

when they are touched with a piece of meat, regular and natural movements of deglutition ensue. In the recent and elaborate experiments of Waller and Prevost, it was shown that, after division of the superior laryngeals, excitation of the parts supplied with sensory filaments by these nerves produced no movements of the pharynx.[1]

The experiments made by galvanizing the trunks of the nerves are extremely interesting. If the nerves be divided and galvanization be applied to their central ends, movements of deglutition are observed, and there is also arrest of the action of the diaphragm. From these experiments, first elaborated by Rosenthal,[2] it would seem that the impression which gives rise to the movements of deglutition aids in protecting the air-passages from the entrance of foreign matters, by temporarily arresting the inspiratory act. These experiments of Rosenthal have been repeated very extensively by physiologists; and concerning the effects of galvanization of the superior laryngeals upon respiration, there is considerable difference of opinion.

The important point for our consideration, in this connection, is the action of the nerves in the ordinary phenomena of deglutition; and in experiments with galvanism, a feeble current simulates most nearly the natural processes. In such experiments, the results have been quite satisfactory. Waller and Prevost used a very feeble current, and confirmed entirely the observations of Rosenthal. They found, also, that galvanization of the roots of the pneumogastrics above the origin of the laryngeals produced the same effects as galvanization of the trunks of the superior laryngeals.[3] The experiments in which a powerful current of

[1] WALLER ET PREVOST, *op. cit.—Archives de physiologie*, Paris, 1870, tome iii., p. 347, *et seq.*

[2] ROSENTHAL, *De l'influence du nerf pneumogastrique et du nerf laryngé supérieur sur les mouvements du diaphragm.—Comptes rendus*, Paris, 1861, tome lii., p. 754; and, *Die Athembewegungen und ihre Beziehungen zum Nervus vagus*, Berlin, 1862, S. 72.

[3] *Loc. cit.*

galvanism was applied to the nerves also show an arrest of respiration; but it is argued that there is nothing special in the action of the superior laryngeals under these conditions, inasmuch as other sensitive nerves have been found to act in the same way.[1] This is undoubtedly true; but it is well known that, in living animals, strong impressions made upon any of the acutely sensitive nerves arrest respiration, and that this is one of the phenomena commonly observed in animals struggling under painful operations. In view of these facts, it seems unnecessary to discuss more fully the numerous experiments on the effects upon respiration of stimulation of the superior laryngeals; and we can assume that it has been demonstrated that an impression made upon the terminal filaments of these nerves, such as occurs in the ordinary process of deglutition, excites, by reflex action, contraction of the constrictors of the pharynx, and, at the same time, momentarily suspends the movements of the diaphragm.

Important experiments have been made within the past few years, upon the action of the pneumogastrics on the circulation, in which it is claimed that nervous filaments, arising, in the rabbit, in part from the trunk of the pneumogastric and in part from the superior laryngeal branch, act as reflex depressors of the vascular tension. These experiments will be fully discussed in connection with the cardiac branches.

Properties and Functions of the Inferior, or Recurrent Laryngeal Nerves.—The anatomical distribution of these nerves shows that their most important function is connected with the muscles of the larynx. The few filaments which are given off in the neck to join the cardiac branches are probably not very important. It is proper to note, however, that it supplies the muscular tissue and mucous membrane of the upper part of the œsophagus and the trachea, and one or two branches are sent to the inferior constrictor of

[1] BERT, *Leçons sur la physiologie comparée de la respiration*, Paris, 1870, p. 459, *et seq.*

the pharynx. The function of these filaments is sufficiently evident.

The inferior laryngeals contain chiefly motor filaments, judging from their distribution as well as from the effects of direct irritation. All who have experimented upon these nerves have noted little or no evidence of pain when they are stimulated or divided.

One of the most important functions of the recurrents is connected with the production of vocal sounds. In another volume, we have fully treated of the mechanism of the voice and the action of the intrinsic muscles of the larynx;[1] and in our account of the physiology of the internal, or communicating branch from the spinal accessory to the pneumogastric, it has been shown that this is the true nerve of phonation.[2] In the older works upon physiology, before the functions of the spinal accessory were fully understood, the experiments on the inferior laryngeals led to the opinion that these were the nerves of phonation, as they showed loss of voice following their division in living animals. It is true that these nerves contain the filaments which preside over the vocal movements of the larynx; but it is also the fact that these vocal filaments are derived exclusively from the spinal accessory, and that the recurrents contain as well motor filaments which preside over movements of the larynx not concerned in the production of vocal sounds.

The muscles of the larynx concerned in phonation are, the crico-thyroids, animated by the superior laryngeals, and the arytencid, the lateral crico-arytenoids, and the thyro-arytenoids, animated by the inferior laryngeals. The posterior crico-arytenoids are respiratory muscles; and it is curious that these are not affected by extirpation of the spinal accessories, but that the glottis is still capable of dilatation, so that inspiration is not impeded. If, however, the spinal accessories be extirpated, and the larynx be then exposed in a living animal, the glottis still remains dilated, but will

[1] See vol. iii., Voice and Speech, p. 490, *et seq.* [2] See page 170, *et seq.*

not close when irritated. If the inferior laryngeals be then divided, the glottis is mechanically closed with the inspiratory act, and the animals often die of suffocation. When we call to mind the varied sources from which the pneumogastrics receive their motor filaments, it is easy to understand how certain of these may preside over the vocal movements, and others, from a different source, may animate the respiratory movements.

As we should naturally expect from what has already been said, section of the inferior laryngeal nerves paralyzes both the vocal and the respiratory movements of the larynx. It is not necessary to refer in detail to the ancient and modern experiments illustrating this point, the former dating from the time of Galen. In adult animals, the cartilages of the larynx are sufficiently rigid to allow of inspiration after the organ has been completely paralyzed; but in young animals, the glottis is closed, and suffocation ensues. We have generally observed in cats, that suffocation follows immediately upon section of the recurrents or of the pneumogastrics in the neck.

The impediment to the entrance of air into the lungs is a sufficient explanation of the increase in the number of the respiratory acts after division of both recurrents. It has been observed by Longet, that the acceleration of respiration is much greater in young than in adult animals. This does not apply to very young animals, in which section of the recurrents produces almost instant death.[1]

Waller and Prevost have shown that feeble galvanization of the central ends of the inferior laryngeals, after their division, produces rhythmical movements of deglutition, generally coincident with arrest of the action of the diaphragm. These phenomena are generally observed in rabbits, but they are not constant.[2] The reflex action of these nerves in

[1] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 533.

[2] WALLER ET PREVOST, *Phénomènes réflexes de la déglutition.—Archives de physiologie*, Paris, 1870, tome iii., p. 346.

deglutition is probably due to the communicating filaments which they send to the superior laryngeal nerves.

Properties and Functions of the Cardiac Nerves, and Influence of the Pneumogastrics upon the Circulation.—One of the most interesting questions connected with the physiology of the pneumogastric nerves is their action upon the heart; and the results of experiments, which will be fully detailed hereafter, are precisely the opposite of what would be expected in the case of a nerve containing motor filaments and distributed to a muscular organ. Section of the pneumogastrics in the neck, far from arresting the action of the heart, increases the rapidity of its pulsations; and galvanization of the nerves arrests the heart's action in diastole.

Within the past few years, some very remarkable experiments have been made upon the influence of certain nerves given off near the superior laryngeals, which have been called the depressors of the circulation; but most observations have been made upon the trunks of the pneumogastrics in the cervical region, as it is exceedingly difficult to isolate the thoracic cardiac branches and to operate upon them without involving other nervous filaments. In galvanizing the nerves in the neck, we have to consider both the direct influence of the current and the phenomena due to reflex action.

Effects of Section of the Pneumogastrics upon the Circulation.—It is not necessary to cite in detail the various experiments upon the effects of section of the pneumogastrics in the neck upon the action of the heart. The division of these nerves in living animals is sufficiently easy, and all who have performed the operation have noted the same results. By section of these nerves, the heart is at once separated from one of the most important of its nervous connections; and the effects show that, as far as this organ is concerned, the motor filaments present great differences from

the ordinary motor nerves of the cerebro-spinal system. Most of the observations made by dividing the nerves have been upon dogs, and the differences in the effects upon other animals are slight and unimportant. The following are the important phenomena presented in typical experiments :

Section of one of the pneumogastrics in the neck does not produce any very marked effect upon the action of the heart, after the slight disturbance which usually follows the operation has passed away. The number of pulsations is slightly increased, and the cardiac pressure, as shown by a cardiometer fixed in the carotid artery, is slightly diminished; but this is insignificant compared with the effects of dividing both nerves.

Section of both pneumogastrics usually produces immediate and serious disturbance in the respirations, which are momentarily accelerated. The animal usually becomes agitated and suffers from want of air; and, when it is desired especially to note the cardiac disturbance, it is often necessary to relieve the respiration by introducing a tube into the trachea. In full-grown dogs, however, the respirations soon become calm, but are diminished in frequency, and are unusually profound. When the animal is in this condition, the beats of the heart are very much increased in frequency, at least doubled; but they are inefficient and tremulous.

An interesting point in this connection is the want of influence of certain medicinal substances over the action of the heart in animals after division of the pneumogastrics. Traube has shown that, while digitalis injected into the veins of a dog was capable in an hour of reducing the pulse to about one-fourth of the normal number of beats per minute, there was no appreciable effect upon the circulation when the injection was made in animals with both pneumogastrics divided.[1]

The influence of the pneumogastrics upon the heart is

[1] TRAUBE, *Versuche über die Wirkung der Digitalis.—Gesammelte Beiträge zur Pathologie und Physiologie*, Berlin, 1871, Bd. i., S. 190, *et seq.*

one of the most interesting points in the physiology of the circulation; but we can discuss the mechanism of the phenomena following section of the nerves more satisfactorily after we have considered the effects of their galvanization.

Effects of Galvanizing the Pneumogastrics or their Branches upon the Circulation.—The experiments upon the effects of galvanization of the pneumogastrics in the neck on the action of the heart are almost innumerable; and, although the explanations of the phenomena observed present the widest differences, the facts themselves are sufficiently simple. These facts will be discussed under the following heads: 1. The direct influence of galvanization of the nerves in the neck, undivided, or of galvanization of the peripheral extremities of the trunks after division. 2. Reflex phenomena following galvanization of the central ends of branches of the pneumogastrics, after their division.

Direct Influence of the Pneumogastrics on the Heart.—In 1846, the brothers Weber noted the important fact that galvanization of the pneumogastrics in the neck rendered the action of the heart slow, and if the galvanization were sufficiently powerful, arrested the heart, which remained flaccid and in diastole for a certain time while the galvanization was continued.[1] This fact has since been confirmed by numerous experimenters, whose observations, however, will not be cited in detail, except as they have developed new and important phenomena.

While there is no difference of opinion among physiologists with regard to the stoppage of the heart by powerful galvanization, it is stated by some that a very feeble current passed through the peripheral ends of the divided nerves quickens the heart's action; but it is admitted by all that it is very difficult to regulate the intensity of the cur-

[1] WEBER, in WAGNER, *Handwörterbuch der Physiologie*, Braunschweig, 1846, Bd. iii., Zweite Abtheilung, S. 42, *et seq.*

rent so as to produce this effect. After section of the nerves, the action of the heart is very readily modified by struggles, etc., on the part of the animal under observation; and, in view of the exceeding nicety of the reported experiments, it cannot be admitted that the heart is capable of being excited to increased rapidity of action, without observations of the most positive character. Such facts are wanting; and furthermore, it has been shown by Dr. Rutherford, in a series of exceedingly exact and satisfactory experiments, that whenever a galvanic current passed through the pneumogastrics has any appreciable effect upon the action of the heart, it is to diminish the frequency of its pulsations.[1] Inasmuch as our object is simply to show that, imitating the nervous force by galvanism, the action of the pneumogastrics is inhibitory, we will not discuss the effects of different currents, and other experiments, which have little relation to the natural action of the nerves, and possess slight interest from a purely physiological point of view.

The direct action of the pneumogastrics upon the heart is undoubtedly through their motor filaments. All the facts developed by experiments are in accordance with this view. If the nerves be divided in the neck, galvanization of the central ends has no effect upon the heart, the pulsations being arrested only when the peripheral ends are stimulated. This shows that, at least as far as the fibres passing down the neck are concerned, the action is centrifugal and direct, not reflex. Another curious fact illustrates the same point very forcibly. It is well known that the woorara-poison completely paralyzes the motor nerves, leaving the muscular irritability and the sensory nerves intact. It has been found that, in animals poisoned with woorara, the action of the heart being maintained by artificial respiration, galvanization of both pneumogastrics has no effect upon its

[1] Rutherford, *Influence of the Vagus upon the Vascular System.—Journal of Anatomy and Physiology*, Cambridge and London, 1869, vol. iii., p. 404, *et seq.*

pulsations.[1] This fact we have repeatedly verified in public demonstrations.[2] Still another curious fact remains bearing on the question under consideration. If powerful galvanization, which immediately arrests the cardiac pulsations, be continued for a certain time, so that the motor filaments become temporarily exhausted and lose their irritability, the heart resumes its contractions, notwithstanding that the galvanization is continued; the nerves being for the time incapable of transmitting the inhibitory influence.[3]

The source of the motor filaments in the pneumogastrics which exert a direct inhibitory action upon the heart becomes an important point to determine. In the original experiments by the brothers Weber, it was shown that, when the galvanic stimulus was applied to that portion of the centres from which the nerves take their origin, the action of the heart was arrested in the same way as when the nerves themselves are galvanized;[4] and it has been shown by subsequent observations, that when the heart is thus arrested by galvanization of the medulla oblongata, if both pneumogastrics be divided in the neck, its action is resumed.[5] This would at first sight lead to the supposition that the inhibitory filaments are derived from the roots themselves of the

[1] Bernard, *Leçons sur les effets des substances toxiques et médicamenteuses*, Paris, 1857, p. 348.

[2] In the inferior classes of animals, there are some exceptional phenomena with regard to the pneumogastrics. In experiments made upon alligators, in New Orleans, in 1861, we found that the action of the heart was promptly arrested by galvanizing the nerves in the neck, when the animal was killed and the general motor nerves were paralyzed by woorara. In some additional experiments, we showed that all of the nerves were not affected by the poison after the same length of time, and that the pneumogastrics were probably the last to come under its influence. (See vol. i., Circulation, 1866, p. 234.) Bernard states, also, that galvanization of the nerves in birds does not affect the heart, a fact for which he offers no explanation. (Bernard, *Système nerveux*, Paris, 1858, tome ii., p. 394.)

[3] Longet, *Traité de physiologie*, Paris, 1869, tome ii., p. 117.

[4] Weber, in Wagner, *Handwörterbuch der Physiologie*, Braunschweig, 1846, Bd. iii., Zweite Abtheilung, S. 42.

[5] Longet, *Traité de physiologie*, Paris, 1869, tome ii., p. 117.

pneumogastrics; but it has been conclusively demonstrated that they are really derived from the spinal accessories, the upper filaments of origin of which are situated just below the roots of the pneumogastrics.

The action of the spinal accessories upon the heart has already been considered.[1] The connection between these nerves and their influence over the heart may be briefly repeated, as follows:

It has been shown that powerful galvanization of one pneumogastric will arrest the heart's action. Waller, after extirpating the spinal accessory nerve upon one side, found that galvanization of the pneumogastric upon that side had no effect upon the heart, provided that from ten to twelve days had elapsed after extirpation of the spinal accessory, a sufficient time to secure disorganization and loss of irritability of its fibres. These experiments show conclusively that the motor filaments contained in the pneumogastric, which act directly upon the heart, are derived exclusively from the communicating branch of the spinal accessory.

Reflex Influence, through the Pneumogastrics, upon the Circulation.—Galvanization of the central ends of the pneumogastrics, after their division in the neck, does not influence the action of the heart, except as the pulsations are affected by the modifications in respiration. In experiments made upon this point by Bernard, the difference in the effects of galvanization of the central and the peripheral ends was distinctly noted. When the central ends were stimulated in dogs, the pupils became dilated, the eyes protruded, sometimes vomiting occurred, and always the number of respiratory acts was diminished, and, with a powerful current, were arrested in inspiration; but the pulsations of the heart were not affected.[2]

[1] See p. 204.

[2] BERNARD, *Système nerveux*, Paris, 1858, tome ii., p. 382, *et seq.*

The arrest of respiration, particularly the action of the diaphragm, was first

Depressor-Nerve.—An important reflex action operating upon the circulation through branches of the pneumogastrics has lately been described by Cyon and Ludwig, in a memoir which received the prize for Experimental Physiology from the French Academy of Sciences, in 1867.[1] The experiments on which this memoir is based are exceedingly clear and satisfactory, and afford, perhaps, the only positive explanation we have of reflex action upon the heart. The substance of these observations is briefly as follows:[2]

In the rabbit is a nerve arising by two roots, one coming from the trunk of the pneumogastric and the other from its superior laryngeal branch, passing then toward the carotid artery and taking its course down the neck by the side of the sympathetic as far as the thorax. In the chest, it joins with sympathetic filaments to pass with them to the heart, by little branches between the origin of the aorta and the pulmonary artery.

This nerve can be completely isolated in the neck from the sympathetic and the trunk of the pneumogastric. If it be divided in this situation, after the irritation produced by the operation has subsided, very distinct and important modifications in the circulation may be produced by its galvanization.

In the first place, it was noted in all the experiments, that galvanization of the peripheral extremities produced no change, either in the number of the pulsations of the heart or in the pressure of blood in the vascular system; which

noted by Traube. (TRAUBE, *Zur Physiologie des Nervus vagus.—Gesammelte Beiträge*, Berlin, 1871, Bd. i., S. 184.)

[1] BERNARD, *Rapport sur un mémoire de* M. E. CYON, *intitulé: de l'action réflexe d'un des nerfs sensibles du cœur.—Journal de l'anatomie*, Paris, 1868, tome v., p. 337.

[2] CYON ET LUDWIG, *Action réflexe d'un des nerfs sensibles du cœur sur les nerfs vaso-moteurs.—Journal de l'anatomie*, Paris, 1867, tome iv., p. 472, *et seq.*

Cyon has lately found in the horse, nerves, in their anatomical and physiological relations, closely resembling the "depressor-nerves" which he first described in the rabbit (*British and Foreign Medico-Chirurgical Review*, London, 1871, No. xcvi., p. 540).

points to the fact that its action is not direct, but reflex, and is due to an impression conveyed to the nerve-centres.

If the central ends of the nerves be galvanized, the pressure in the arteries diminishes little by little, until it may be reduced to one-half or two-thirds of the pressure before the irritation was applied. This low pressure continues so long as the interrupted current is applied; but when the galvanization is arrested, it gradually returns to the normal standard. These phenomena are observed in all the large arterial trunks. The length of time required to produce the greatest diminution in the pressure is somewhat variable, but the experimenters have never seen it reach its minimum before fifteen pulsations of the heart.

"The diminution in the pressure is attended with a reduction of the pulse in the instances in which the depressor-nerve only has been divided. The irritated nerve is isolated in a manner so complete that we cannot fear the passage of the exciting current in the trunk of the pneumogastric. The changes in the number of pulsations persist even when the pneumogastric has been excited by the side where the irritation has been applied, from the point where the superior laryngeal is given off to the point where the pneumogastric enters the thoracic cavity.

"From the foregoing it is evident that the changes taking place in the number of pulsations are due to excitation of the depressor-nerve. If we study attentively the progress of the cardiac pulsations during the excitation, we observe always that the most considerable reduction takes place at the beginning of the experiment; that is to say, at the moment when the blood-pressure descends from its normal standard to the lowest point. When the pressure is completely depressed, the pulse is accelerated again and even reaches almost completely the numbers presented before the oscillations. When the irritation ceases, after a shorter or longer period, the heart generally beats more rapidly than before the irritation, and this during all the time that

is occupied in the return of the pressure to the normal standard. This observation in itself refutes the idea that the diminution in the pressure may depend upon the diminished number of pulsations. If the reduction in the rate of the pulse produced a diminished pressure, it should be increased when the pulsations of the heart become accelerated.

"The manner in which the pulse is reduced leads to the supposition that it is due to a reflex action of the pneumogastric.

"It was easy to verify this last opinion, and we have been able to confirm it by first cutting the pneumogastrics on both sides, and afterward irritating the central end of the depressor-nerve. In this case, the pressure fell to 0.62, 0.55, etc., while the number of pulsations remained the same, or at least oscillated very slightly above and below the number observed before the irritation."

The above extract from the observations of Cyon shows two important points:

First, galvanic stimulation of the central extremities of the divided depressor-nerves reduces the number of pulsations of the heart by a reflex action; the impression being conveyed to the nerve-centres by the depressor-nerves, the force acting directly upon the heart being transmitted through efferent filaments in the trunk of the pneumogastric.

Second, the reduction in the pressure of blood in the larger arteries is independent of the efferent filaments of the pneumogastric, and bears no relation to the reduction in the number of cardiac pulsations.

It now remains to explain, if possible, the mechanism of the reduction in the arterial pressure. This question is treated by Cyon by the method of exclusion. The diminution in the pressure followed galvanization of the central extremities of the depressor-nerves, even when the heart was removed from its influence by section of both pneumogastrics in the neck, and when all the voluntary movements and the movements of respiration were abolished by poison-

ing with woorara. In the latter case, the circulation was kept up by artificial respiration.

Without following out the various observations which go to show that the influence of the depressor-nerve upon the arterial pressure is independent of the force or frequency of the heart's action, and is due to some cause which operates upon the vessels themselves, we will simply give the results of the experiments upon the splanchnic nerves. If the abdomen be opened, and one or more of these nerves be divided, the arterial pressure is immediately diminished. After this, if the peripheral extremities of the divided nerves be galvanized, the pressure rapidly returns to the normal standard. These experiments "demonstrate that the splanchnic nerves constitute the most important vaso-motor nerves in the entire organism."

This point being settled, the depressor-nerves were galvanized after section of the splanchnic nerves, in some cases exaggerating the general arterial pressure by compressing the aorta, and in others, leaving the aorta free. "The irritation of the depressor-nerve after section of the splanchnic nerve produced still a diminution in the blood-pressure, but the absolute value of this diminution is much less than it was during the irritation of the depressor-nerve before the section of the splanchnic."

These experiments show pretty conclusively that the diminished pressure in the arterial system following stimulation of the central ends of the depressor-nerves after division is due to a reflex action on the blood-vessels of the abdominal organs, taking place through the splanchnic nerves. We are sufficiently familiar with reflex paralyzing action upon the blood-vessels through the sympathetic system; and when we call to mind the immense extent of the abdominal vascular system, we can readily understand how, if the resistance to the flow of blood be diminished by paralysis of the muscular coats of the small arteries, the pressure in the larger arteries would be reduced.

Mechanism of the Influence of the Pneumogastrics upon the Action of the Heart.—It is useless to speculate upon the exact mechanism of the action of the pneumogastrics upon the heart. Although various explanations have been presented of the effects following division of the nerves in the neck, and of the opposite phenomena which attend the galvanization of their peripheral ends, they are all more or less unsatisfactory. All that can be said, in the present state of our knowledge, is, that the pneumogastrics have a direct inhibitory influence on the heart. When they are divided, and the heart is removed from their influence, the pulsations become more rapid. When the peripheral ends of the divided nerves are galvanized, the heart beats more slowly, or its action may be arrested by a current of sufficient power. This action may also be reflex, due to an impression conveyed to the centres by what have been described by the brothers Cyon and Ludwig, as the depressor-nerves.

Properties and Functions of the Pulmonary Branches, and Influence of the Pneumogastrics upon Respiration.—The trachea, bronchi, and the pulmonary structure are supplied with motor and sensory filaments by branches of the pneumogastrics. The recurrent laryngeals supply the upper, and the pulmonary branches, the lower part of the trachea, the lungs themselves being supplied by the pulmonary branches alone. The sensibility of the mucous membrane of the trachea and bronchi is due to the pneumogastrics, for these parts are insensible to irritation when the nerves have been divided in the neck. Longet has shown that, while an animal coughed and showed signs of pain when the mucous membrane of the respiratory passages was irritated, after division of the pneumogastrics there was no evidence of sensibility, even when the tracheal mucous membrane was treated with strong acid, or even cauterized. He also saw the muscular fibres of the small bronchial tubes

contract when a galvanic stimulus was applied to the branches of the pneumogastrics.[1]

The main interest, in this connection, is attached to the pulmonary branches and their relations to the respiratory acts. These are undoubtedly connected with important reflex phenomena, acting as centripetal nerves; and their direct action in respiration is probably much less important. They are exposed and operated upon in living animals with so much difficulty, that we know little of the direct effects of their irritation, and must judge of their general properties chiefly by experiments showing their action upon respiration. We shall have to study, in connection with the functions of these nerves, the effects of their division upon the lungs and the respiratory acts, and the phenomena, referable to the respiratory organs, which follow their galvanization. We shall also consider certain theoretical views with regard to their action in the automatic processes of respiration, and with the sense of want of air (*besoin de respirer*), which gives rise to the reflex respiratory acts.

Effects of Division of the Pneumogastrics upon Respiration.—Section of both pneumogastrics in the neck, in mammals and birds, is usually followed by death, in from two to five days. In young animals, death may occur almost instantly, from paralysis of the respiratory movements of the glottis, a fact which we have already noted in connection with the recurrent laryngeal nerves.[2] In this connection, we may note an interesting fact observed by Prof. J. C. Dalton, of New York, who has succeeded in keeping dogs alive after division of both pneumogastrics in the neck until complete recovery took place. In several instances of this kind, after killing the animals, Prof. Dalton found complete reunion of the divided ends.[3]

Very little of importance, with regard to the functions of

[1] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 535.
[2] See page 222.
[3] Oral communication.

the pneumogastrics in connection with respiration, has been ascertained by the numerous experiments on record of section of one or both of these nerves in the cervical region. It has been found by all experimenters, that animals survived, and presented no very distinct abnormal phenomena, after section of one nerve. Longet states that animals operated upon in this way present hoarseness of the voice and a slight increase in the number of respiratory acts. Some observers have found the corresponding lung partly emphysematous and partly engorged with blood, and others have not noted any change in the pulmonary structure.[1]

When both nerves are divided in full-grown dogs, an experiment which we have often repeated, the effect upon the respiratory movements is very marked. For a few seconds, the number of respiratory acts may be increased; but as soon as the animal becomes tranquil, the number is very much diminished, and the movements change their character. The inspiratory acts become unusually profound, and are attended with excessive dilatation of the thorax. The animal is generally quiet and indisposed to move. We have seen, under these conditions, the number of respirations fall from sixteen or eighteen to four per minute.

In most animals that die from section of both pneumogastrics, the lungs are found engorged with blood, and, as it were, carnified, so that they sink in water. This curious fact was noted by Legallois;[2] and although its physiological significance is not apparent, it has been the subject of much speculation and experimental research. Many attempts have been made to account for this peculiar condition. Traube supposed that it was due to the penetration of secretions into the respiratory passages;[3] but this was disproved by

[1] LONGET, *Anatomie et physiologie du système nerveux*, Paris, 1842, tome ii., p. 349, *et seq.*

MAGENDIE, *Phénomènes physiques de la vie*, Paris, 1842, tome i., p. 204.

[2] LEGALLOIS, *Œuvres*, Paris, 1824, tome i., p. 194.

[3] TRAUBE, *Die Ursachen und die Beschaffenheit derjenigen Veränderungen*,

Bernard, who has presented by far the most satisfactory explanation of this condition.

Bernard found that the pulmonary lesion did not exist in birds, although section of both nerves was fatal. It had previously been ascertained that, in some animals, death takes place with no alteration of the lungs.[1] When the entrance of the secretions into the air-passages was prevented by the introduction of a canula into the trachea, the carnification of the lungs was nevertheless observed. Without detailing all of the experiments upon which the explanation offered by Bernard is based, it is sufficient to state that he observed a traumatic emphysema as a consequence of the excessively labored and profound inspirations. Indeed, this can be actually seen when the pleura is exposed in living animals. As a result of this distention of the air-cells, the pulmonary capillaries are ruptured in different parts, the blood becomes coagulated, and the lungs are finally carnified. This cannot occur in birds, because the lungs are fixed, and their relations are such that they are not exposed to excessive distention in inspiration.[2]

There is no satisfactory explanation of the remarkable changes in the respiratory movements that follow section of the pneumogastrics.

Sense of Want of Air.—The pneumogastrics may regulate the respiratory acts, but they are not the medium through which the sense of want of air (*besoin de respirer*), which gives rise to the reflex movements of respiration, is conveyed to the nerve-centres. If it be true, as it undoubtedly is, that section of both pneumogastrics in the neck modifies the number and the character of the respirations, and that, after division of the nerves, galvanization of their central ends arrests respiration, it is more than probable

welche das Lungenparenchym nach Durchschneidung der Ner. vagi erleidet.—Gesammelte Beiträge zur Pathologie und Physiologie, Berlin, 1871, Bd. i., S. 80.

[1] BERNARD, *Système nerveux*, Paris, 1858, tome ii., p. 353.

[2] BERNARD, *op. cit.*, p. 368.

that this function is normally influenced through these nerves, by impressions conveyed to the centres; but precisely what this influence is, or what is the mechanism of its action, we do not know.

The positive statement that the sense of want of air is not conveyed to the nerve-centres through the pneumogastrics is based, to a great extent, upon our own experiments, which have been fully detailed in another volume;[1] and we will here give simply their results and the conclusions to which they lead.

The acts of respiration are involuntary, though they may be modified, within certain limits, through the will; and they are reflex, due to an impression conveyed to the respiratory nervous centre, the medulla oblongata, which gives rise to the stimulus that excites the action of the inspiratory muscles. It has been conclusively shown by experiments, the first being those of Robert Hook,[2] that if artificial respiration be efficiently carried on in a living animal, so as to supply air fully to the system, the sense of want of air is not appreciated, and the animal makes no effort to breathe; but if respiration be imperfectly performed, the animal almost immediately feels the want of air, and, in our experiments, the exposed respiratory muscles were thrown into violent but ineffectual contraction.

The principal points with reference to the location of the sense of want of air and its transmission to the nerve-centres, developed by our own experiments, are the following:

A dog was etherized, the chest was opened, exposing the heart and lungs, and artificial respiration was carried on by means of a bellows secured in the trachea. So long as the supply of air was sufficient, the animal made no effort to breathe, even when allowed to come from under the influence of the anæsthetic.

[1] See vol. i., Respiration, p. 479, *et seq.*

[2] *An Account of an Experiment made by Mr. Hook, of Preserving Animals alive by Blowing through their Lungs with Bellows.—Philosophical Transactions*, London, 1667, vol. ii., p. 539.

An artery was then exposed and the color of the blood noted. When the artificial respiration was arrested, the animal made efforts to breathe as soon as the blood became dark in the arterial system. We concluded from this, that the impression conveyed to the respiratory nervous centre, giving rise to the movements of respiration, was due to the action of the non-oxygenated blood.

To ascertain whether the impression were made upon the nerves distributed to the lungs or upon other nerves, a large vessel was divided and the system was drained of blood, the lungs being continually supplied with fresh air. In this case, respiratory efforts of the most violent character were invariably noted following the hæmorrhage. This portion of the experiment demonstrated that the sense of want of air was not dependent upon the accumulation of carbonic acid in the lungs, but was due to a deficient supply of the oxygen-carrying fluid to the general system. It further demonstrated that the impression in the general system was not due to the presence of carbonic acid, but to the absence of oxygen; for no blood containing carbonic acid circulated in the system.

These phenomena were observed without any modification, after division of both pneumogastric nerves in the neck, and they seem to prove conclusively that the sense of want of air is not transmitted to the respiratory nervous centre through the medium of these nerves.[1]

Effects of Galvanization of the Pneumogastrics upon Respiration.—The phenomena which follow galvanization of the pneumogastrics, though they are curious and interesting, do not throw much light upon the relations of these

[1] For a full account of these experiments, with their bearing upon certain respiratory phenomena before birth, the reader is referred to the original article, entitled, *Experimental Researches on Points connected with the Action of the Heart and with Respiration*, published in the *American Journal of the Medical Sciences*, Philadelphia, October, 1861. Since this publication, the experiments have been frequently repeated in public demonstrations, and the conclusions verified.

nerves to respiration. We have already mentioned the arrest of the respiratory movements by galvanization of the superior laryngeal branches and of the central ends of the nerves after their division in the neck.[1] The main point of interest in this connection is the fact that the effects observed are entirely reflex, galvanization of the peripheral ends of the divided nerves having no direct action on the movements of the thorax.

In view of the very indefinite physiological applications of the experiments made by galvanizing the nerves, we will not give in detail the numerous observations upon this subject, but simply state the results, as given in a recent and very elaborate work on respiration, by M. Bert:[2]

"1. Respiration may be arrested by excitation of the pneumogastrics (Traube), of the larynx (Cl. Bernard), of the nostrils (M. Schiff), of most of the sensory nerves (M. Schiff, an assertion that I have not been able to verify).

"2. This arrest may take place either in inspiration or in expiration, through any one of these nerves, without attributing it to the action of derived currents.

"3. A feeble excitation accelerates the respiration; a more powerful excitation retards it; a very powerful excitation arrests it. These words 'feeble' and 'powerful' having, it is understood, only a relative sense for any one animal and under certain conditions: what is feeble for one would be powerful for another, etc.

"I believe, in opposition to the opinion of Rosenthal, that section of the pneumogastrics does not increase the difficulty of arresting respiration; at least, death by excitation occurs much more easily in this case.

"4. When the respiratory movements are completely arrested, it is always the same for the general movements of the animal, which remains motionless.

[1] See page 219.

[2] BERT, *Leçons sur la physiologie comparée de la respiration*, Paris, 1870, p. 489, *et seq.*

"5. Respiration returns even during excitation, and when this is arrested, it almost always becomes accelerated.

"6. Arrest in expiration is more easily obtained than arrest in inspiration; there are animals, indeed, in which it is impossible to effect the latter.

"7. If an excitation be employed sufficiently powerful to arrest respiration in inspiration, all respiratory movements may be made to cease at the very moment when the excitation is applied (inspiration, half-inspiration, expiration), either by operating on the pneumogastric, or operating upon the laryngeal. . . .

"Any feeble excitation of centripetal nerves increases the number of the respiratory movements; any powerful excitation diminishes them. A powerful excitation of the pneumogastrics, of the superior laryngeal, of the nasal branch of the infra-orbital, may arrest them completely; if the excitation be sufficiently energetic, the arrest takes place at the very moment it is applied. Finally, sudden death of the animal may follow a too powerful impression, thus transmitted to the respiratory centre: all this being true for certain mammalia, birds, and reptiles."

The above formulated statements express the experimental facts at present known with regard to the influence of the pneumogastrics upon respiration. The pulmonary branches themselves are so deeply situated that they have not as yet been made the subject of direct experiment, with any positive and satisfactory results. A theory has recently been proposed in which it has been assumed that there are two kinds of nerves in the pulmonary branches of the pneumogastrics, one set being excited by inflation of the lungs, which excitation gives rise to expiration, the other set being stimulated by collapse of the lungs, which excites inspiration; but the experiments upon which this idea is based are vague and unsatisfactory.[1]

[1] HERING, *Die Selbststeurung der Athmung durch den Nervus vagus.—Sitzungsberichte der mathematisch-naturwissenschaftlichen Classe der k. Akademie der Wissenschaften*, Wien, 1868, Bd. lvii., 2 Abtheilung, S. 672, *et seq.*

Properties and Functions of the Œsophageal Nerves.— The muscular walls and the mucous membrane of the œsophagus are supplied entirely by branches from the pneumogastrics. The upper portion is supplied by filaments from the inferior laryngeal branches, the middle portion, by filaments from the posterior pulmonary branches, and the inferior portion receives the œsophageal branches. These branches are both sensory and motor; but probably the motor filaments largely predominate, for the mucous membrane, though it is sensible to the extremes of heat and cold, the feeling of distention, and a burning sensation upon the application of strong irritants, is by no means acutely sensitive.

That the movements of the œsophagus are animated by branches from the pneumogastrics, has been clearly shown by experiments. In the first place, except in animals in which the anatomical distribution of the nerves is different from the arrangement in the human subject, the entire œsophagus is paralyzed by dividing the nerves in the neck. In a series of very elaborate experiments, by Chauveau, it was shown that section of the nerves in the cervical region paralyzed the entire length of the œsophagus in rabbits, but, owing to a peculiar distribution of the nerves in dogs, the section paralyzed only the terminal portion.[1]

According to Bouchardat and Sandras,[2] Longet, and others, when the pneumogastrics are divided in the cervical region, in dogs, if the animals attempt to swallow a considerable quantity of food, the upper part of the œsophagus is found enormously distended.[3] Bernard noted, in a dog in which a gastric fistula had been established, that articles of food given to the animal did not pass into the stomach,

[1] Chauveau, *Du nerf pneumogastrique considéré comme agent excitateur et comme agent coördinateur des contractions œsophagiennes.—Journal de la physiologie*, Paris, 1862, tome v., p. 342.

[2] Bouchardat et Sandras, *Expériences sur les fonctions des nerfs pneumogastriques dans la digestion.—Comptes rendus*, Paris, 1847, tome xxiv., p. 59.

[3] Longet, *Traité de physiologie*, Paris, 1869, tome iii., p. 547.

though he made great efforts to swallow. An instant after the attempt, the matters were vomited, mixed with mucus, but of course did not come from the stomach.[1]

Direct experiments upon the roots of the pneumogastrics have shown that these nerves influence the movements of the œsophagus, and that their motor filaments are not derived from the spinal accessory. Chauveau states, as the result of numerous observations, that "the œsophagus contracts throughout its entire length when the roots of the pneumogastrics are excited;—it never contracts when the bulbar roots of the spinal accessory are excited.[2]

Properties and Functions of the Abdominal Branches.—In view of the very extensive distribution of the terminal branches of the pneumogastrics to the abdominal organs, it is evident that the functions of these nerves must be very important, particularly since it has been shown that the right nerve is distributed to the whole of the small intestine. We shall consider the functions of these branches in their relations to the liver, the stomach, and the intestines. We have no positive information with regard to their action upon the spleen, kidneys, and suprarenal capsules.

Influence of the Pneumogastrics upon the Liver.—There is very little known with regard to the influence of the pneumogastrics upon the secretion of bile. The only positive statements to be found on this subject are those of Longet.[3] This physiologist has repeatedly remarked, after section of the pneumogastrics, that the bile diminishes in density and contains less coloring matter than under normal conditions. This he attributes to disturbances in the hepatic circulation, by which a serous fluid is exuded and mixes with the bile.

[1] Bernard, *Système nerveux*, Paris, 1858, tome ii., p. 422.

[2] Chauveau, *Du nerf pneumogastrique, etc.—Journal de la physiologie*, Paris, 1862, tome v., p. 205.

[3] Longet, *Traité de physiologie*, Paris, 1869, tome iii., p. 552.

The disturbances in the circulation are somewhat similar to those occasionally observed in the lungs. The vessels are strongly injected, and sometimes contain clots of blood. The hepatic tissue is more friable than usual, and presents a greenish-black color.

The most important experiments upon the innervation of the liver are those of Bernard, and relate to its glycogenic function. We shall have little to say on this subject, however, in addition to what we have already stated in treating of the liver as a sugar-producing organ.[1] The view which we have advanced with regard to the glycogenic function is that the liver is constantly producing sugar during life, which is completely washed out by the blood in its passage through this organ, which itself contains little or no sugar, under normal conditions. With this view, we are to look for sugar in the blood, in certain situations, and not in the liver itself; though after death, a change of the glycogenic matter in the liver into sugar takes place with great rapidity, and sugar may then be found in its tissue. Normally, sugar disappears in the lungs, and is not found in the blood of the arterial system. The presence of sugar in the urine is abnormal.

Bernard found that if both pneumogastrics be divided in the neck, and the animal be killed at a period varying from a few hours to one or two days after, the liver contains no sugar, under the conditions in which he generally found it; *i. e.*, a certain time after death. From experiments of this kind, he concludes that the glycogenic function is suspended when the nerves are divided.[2] The experiments, however, made by irritating the pneumogastrics, are more satisfactory, as in these he looked for sugar in the blood and in the urine, and did not confine his examinations to the substance of the liver.

After division of the pneumogastrics in the neck, if the

[1] See vol. iii., Secretion, p. 324, *et seq.*

[2] BERNARD, *Leçons de physiologie expérimentale*, Paris, 1855, p. 324.

peripheral ends be galvanized, there is no effect upon the liver; but if galvanization be applied to the central ends, the glycogenic function becomes exaggerated, and sugar makes its appearance in the blood and in the urine. Bernard has made a number of experiments illustrating this point, upon dogs and rabbits. The galvanic current employed was generally feeble, and was continued for from five to ten minutes, two or three times in an hour; in some instances, the irritation was kept up for thirty minutes.[1] From these experiments, it is assumed that the physiological production of sugar by the liver is reflex, and is due to an impression conveyed to the nerve-centres through the pneumogastrics. A very interesting and adroit experiment by the same observer shows that section of the pneumogastrics between the lungs and the liver does not affect the production of sugar. This delicate operation is performed by making a valvular opening in the chest, preventing the ingress of air by suddenly forcing the finger into the wound, and then introducing a long, delicate hook with a cutting edge, and dividing the nerves, which may be reached by the finger in small dogs, and feel like tense cords by the side of the œsophagus. We have already noted, in another volume,[2] the fact observed by Bernard and by Pavy, that the inhalation of irritating vapors and of anæsthetics produces a hypersecretion of sugar.

The remarkable effects of irritating the floor of the fourth ventricle, by which we can produce temporary diabetes, have been considered fully in connection with the glycogenic function of the liver. This effect is not due to a direct transmission of the irritation to the liver through the pneumogastrics, for the phenomena of hypersecretion are observed in animals upon which this operation has been performed after section of both pneumogastrics in the neck. It is prob-

[1] BERNARD, *Leçons de physiologie expérimentale*, Paris, 1855, p. 325; and *Système nerveux*, Paris, 1858, p. 437, *et seq.*

[2] See vol. iii., Secretion, p. 327.

able, indeed, that the impression is conveyed to the liver through the sympathetic system, for it has been shown by Schiff and Longet, that animals do not become diabetic after irritation of the floor of the fourth ventricle, when the branches of the sympathetic going to the solar plexus have been divided.[1] The operation, however, of dividing the sympathetic nerves in this situation is so serious, that it may interfere with the experiment in some other way than by the direct influence of the nerves upon the liver.

Influence of the Pneumogastrics upon the Stomach and Intestines.—The number of observations that have been made upon the influence of the pneumogastric nerves on digestion in the stomach is immense, and many of the earlier experiments were quite contradictory. We do not propose, however, to treat of this subject from a purely historical point of view, for the reason that, before 1842 and 1843, when gastric fistulæ were first established in living animals, by Bassow and Blondlot, little was known of the normal movements of the stomach and of the mechanism of the secretion of the gastric juice; and farther, before the observations of Bouchardat and Sandras, in 1847, the effects of section of the nerves in the neck upon the action of the œsophagus in deglutition were not understood. If we study the literature of the subject anterior to 1842, we find a great deal of confusion, due to the facts just stated. Longet, in his work on the nervous system, published in 1842, gives an excellent account of the various experiments up to that date. He cites a great number of authors, Bichat, Tiedemann and Gmelin, Bischoff, Schultz, Breschet and Milne Edwards, Magendie, Müller, Mayo, and many others, to whom we will not refer in detail.[2] Leaving out of the question, then, most of the earlier experiments, we shall treat of the influence of

[1] Longet, *Traité de physiologie*, Paris, 1869, tome iii., p. 553.

[2] Longet, *Anatomie et physiologie du système nerveux*, Paris, 1842, tome ii., p. 320, *et seq.*

the pneumogastrics upon the stomach and intestines, under the following heads:

1. The effects of galvanization of the nerves.

2. The effects of section of the nerves upon the movements of the stomach in digestion.

3. The effects of section of the nerves upon the secretion of the gastric juice and the chemical processes of digestion.

4. The influence of the nerves upon the small intestine.

Effects of Galvanization.—Bichat, in the first edition of his great work on general anatomy, published in 1801, states distinctly that irritation of the pneumogastrics produces contraction of the muscular coat of the stomach: "I remark nevertheless that irritation of one of the vagus nerves, or of both, immediately causes the stomach to contract, as occurs in a voluntary muscle the nerve of which is irritated. It is necessary, in performing this experiment, to open the abdomen of the living animal, and then to irritate the eighth pair in the cervical region, in order to have under the eyes the organ that is made to contract."[1] This fact was confirmed by Tiedemann and Gmelin,[2] and many others, but was denied by Müller.[3] In more recent experiments, the effects of galvanization of the pneumogastrics upon the movements of the stomach are unquestionable. Longet shows that the stomach contracts as a consequence of irritation of the nerves, not instantly, but after the lapse of five or six seconds. He explains some of the contradictory results obtained by other observers by the fact that these contractions are very marked during stomach-digestion, while they are wanting "when the stomach is entirely empty,

[1] Bichat, *Anatomie générale, appliquée à la physiologie et à la pathologie*, Paris, 1801, séconde partie, tome iii., p. 360.

[2] Tiedemann et Gmelin, *Recherches expérimentales, physiologiques et chimiques, sur la digestion*, Paris, 1827, première partie, p. 374.

[3] Müller, *Elements of Physiology*, London, 1840, vol. i., p. 550.

retracted on itself and in a measure in repose." According to the same author, irritation of the splanchnic nerves, while it produces movements of the intestines, does not affect the stomach. Judging from the tardy contraction of the stomach and the analogy between the action of the pneumogastrics upon this organ and the action of the sympathetic nerves upon the non-striated muscular tissue, Longet assumes that the motor action of the pneumogastrics is due, not to the proper filaments of these nerves, but to filaments derived from the sympathetic system. "This interpretation removes the singular physiological anomaly that an organ, the action of which is entirely removed from the control of the will, should depend upon a voluntary, or cerebro-spinal nerve."[1] This explanation of the contradictory results of experiments and of the mechanism of the action of the pneumogastrics upon the stomach seems entirely satisfactory, and may be accepted without reserve.

Effects of Section of the Pneumogastrics upon the Movements of the Stomach.—If the pneumogastrics be divided in the neck in a dog in full digestion, in which a gastric fistula has been established so that the interior of the organ can be explored, the following phenomena are observed:

In the first place, before division of the nerves, the mucous membrane of the stomach is turgid, its reaction is intensely acid, and, if the finger be introduced through the fistula, it will be firmly grasped by the contractions of the muscular walls. When the pneumogastrics are divided, under these conditions, the contractions of the muscular walls instantly cease, the mucous membrane becomes pale, the secretion of gastric juice is apparently arrested, and the sensibility of the organ is abolished.[2] Paralysis of the stomach, etc., had been noted,[3] long before the observations of Ber-

[1] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 546.

[2] BERNARD, *Système nerveux*, Paris, 1858, tome ii., p. 422.

[3] TIEDEMANN ET GMELIN, *Recherches sur la digestion*, Paris, 1827, première partie, p. 373.

nard; but his experiments on animals with a fistulous opening into the stomach are the most striking.

Notwithstanding the apparent arrest of the movements of the stomach in digestion by section of the pneumogastrics, experiments carefully performed show that substances may be very slowly passed to the pylorus, and that the movements, though they are immensely diminished in activity, are not entirely abolished. This fact has been established beyond question by the experiments of Schiff, who attributes the movements occurring after section of the nerves to local irritation of the intramuscular terminal nervous filaments.[1]

Effects of Section of the Pneumogastrics upon Digestion, etc.—Since the publication of the second volume of this work, in which we considered briefly the action of the pneumogastrics in digestion, we have reviewed the literature of the subject, as well as the publications that have appeared since that time, but we find little, if any thing, to add to the statements already made.[2] The facts with regard to the effects of division of the nerves in the cervical region upon the secretion of gastric juice are briefly as follows:

When both nerves are divided, while an animal is in full digestion, the mucous membrane becomes pale and flaccid, and the secretion of gastric juice is apparently arrested at once; but if the animal survive the operation for a day or two, a small quantity of juice may be secreted as the result of local stimulation, and digestion of a very small quantity of food, finely divided and introduced into the stomach by a fistulous opening, may take place.[3] A serious difficulty in the digestion of large masses of food after division of the nerves is due to the cessation of the movements of the stomach. It is stated by Tiedemann and Gmelin, that di-

[1] Schiff, *Leçons sur la physiologie de la digestion*, Florence et Turin, 1867, tome ii., p. 389.

[2] See vol. ii., Digestion, p. 283.

[3] Longet, *Traité de physiologie*, Paris, 1869, tome iii., p. 549.

gestion may be to a certain extent reëstablished, under these conditions, by galvanizing the peripheral extremities of the divided nerves.[1]

There is very little to be said with regard to the relations of the pneumogastrics to the sensations of hunger and thirst. It would be very natural to infer, from the distribution of these nerves to the mucous membrane of the stomach, that they should be involved in these sensations; but in treating of this subject elaborately, in connection with alimentation, we have shown that hunger and thirst really have their origin in the general system, though the sensations are referred subjectively to the stomach and fauces, and that, in all probability, the sensations persist after division of both pneumogastrics.[2]

With regard to the influence of the pneumogastrics upon absorption from the stomach, we have also mentioned the fact, demonstrated by Longet, that the passage of poisons from the stomach into the blood-vessels may be retarded by section of the nerves, but is not prevented.[3]

Physiologists have given but little attention to the influence of the pneumogastrics upon the intestinal canal, for the reason that the distribution of the abdominal branches to the small intestine, notwithstanding the researches of Kollmann, in 1860, does not appear to be generally recognized. The right, or posterior abdominal branch was formerly supposed to be lost in the semilunar ganglion and the solar plexus, after sending a few filaments to the stomach; but since it has been shown that this nerve is supplied to the whole of the small intestine,[4] its physiology, in connection with intestinal secretion, has assumed considerable importance.

In an admirable series of experiments, by Prof. Horatio C. Wood, Jr., of Philadelphia, the importance of the abdomi-

[1] Tiedemann et Gmelin, *Recherches sur la digestion*, Paris, 1827, première partie, p. 373.

[2] See vol. ii., Alimentation, p. 14.

[3] See vol. ii., Absorption, p. 468.

[4] See p. 211.

nal branches of the right nerve is fully illustrated.[1] These experiments show, in the most conclusive and satisfactory manner, that the pneumogastrics influence intestinal as well as gastric secretion. One of the most interesting and curious points in connection with their function is, that after section of the nerves in the cervical region, the most powerful cathartics, croton-oil, calomel, podophyllin, jalap, arsenic, etc., fail to produce purgation, even in doses sufficient to cause death. The articles used were either given by the mouth, just before dividing the nerves, or were injected under the skin.

Though the observations of Dr. Wood are not entirely new, they are by far the most extended and satisfactory, and were made with a knowledge of the fact of the distribution of the nerves to the small intestine. Dr. Wood quotes freely from the experiments made by Sir Benjamin Brodie[2] and by Dr. John Reid.[3] Brodie failed to produce purging in dogs when both pneumogastrics had been divided in the neck after the administration of arsenic by the mouth and injecting it under the skin. Dr. Reid made five experiments, and in all but one, it is stated that diarrhœa existed after division of the nerves. In twenty experiments by Dr. Wood, there was no purgation after division of the nerves, in one there was free purgation, and in one there was "some slight muco-fecal discharge." From these, Dr. Wood concludes, that while section of the cervical pneumogastrics, in the great majority of instances, arrests gastro-intestinal secretion and prevents the action of purgatives upon the intestinal canal,

[1] Wood, *On the Influence of Section of the Cervical Pneumogastrics upon the Action of Emetics and Cathartics.—American Journal of the Medical Sciences*, Philadelphia, 1870, New Series, vol. lx., p. 75, *et seq.*

[2] Brodie, *Experiments and Observations on the Influence of the Nerves of the Eighth Pair on the Secretions of the Stomach.—Philosophical Transactions*, London, 1814, vol. xiv., p. 104.

[3] Reid, *Experimental Investigation into the Functions of the Eighth Pair of Nerves.—Physiological, Anatomical, and Pathological Researches*, London, 1848, p. 245, *et seq.*

a few exceptional cases occur in which these effects are not observed.

The facts just mentioned are exceedingly interesting in connection with the experiments of Traube upon the action of digitalis after section of the pneumogastrics. It will be remembered that, in these experiments, digitalis failed to diminish the number of beats of the heart when the nerves had been divided in the neck, showing that the separation of the heart from its connections with the cerebro-spinal system removed the organ from the peculiar and characteristic effects of the poison.[1]

It would be interesting to determine whether the pneumogastrics influence the intestinal secretions through their own fibres or through filaments received from the sympathetic system; but there are no experimental facts sufficiently definite to admit of a positive answer to this question. If the action take place through the sympathetic system, as in the case of the stomach, the filaments of communication join the pneumogastrics high up in the neck, and become incorporated with the true fibres of the nerve in its trunk.

Summary of the Distribution, Properties, and Functions of the Pneumogastrics.—The pneumogastrics have their apparent origin from the lateral portion of the medulla oblongata, just behind the olivary bodies, between the roots of the glosso-pharyngeals and the spinal accessories. Their deep origin is mainly from the gray substance in the floor of the fourth ventricle. In their course, they each present two ganglia, the ganglion of the root and the ganglion of the trunk. They pass out of the cranial cavity on either side, by the posterior foramen lacerum, with the glosso-pharyngeals, the spinal accessories, and the internal jugular veins.

The nerves receive anastomosing branches from the spinal accessories, facials, sublinguals, the anterior roots of the upper two cervicals, and the sympathetic. The nerves fre-

[1] See p. 224.

quently send branches to the glosso-pharyngeals; and filaments joining others from the glosso-pharyngeals, the spinal accessories, and the sympathetic, go to form the pharyngeal plexus.

From above downward, the branches of the pneumogastrics are the following:

1. The auricular, distributed to the integument of the upper portion of the external auditory meatus and to the membrana tympani.

2. The pharyngeal, containing motor filaments derived from the spinal accessory, distributed to the muscles and mucous membrane of the pharynx.

3. The superior laryngeals, distributed to the mucous membrane of the epiglottis, base of the tongue, aryteno-epiglottidean folds, ventricles of the larynx and lining membrane as far as the true vocal cords, and to the crico-thyroid muscle. From these nerves and the main trunk of the pneumogastrics, arise the so-called depressor-nerves of the circulation.

4. The inferior laryngeals, turning around the great vessels at the top of the thorax, pass up the neck, sending filaments to the upper part of the œsophagus, trachea, and the inferior constrictors of the pharynx, their terminal branches supplying all of the muscles of the larynx except the crico-thyroids.

5. The cervical and thoracic cardiac branches, going to the cardiac plexus, to be distributed to the heart.

6. The anterior and posterior pulmonary branches, distributed to the pulmonary tissue, following out the bronchial tree to its minutest ramifications, and sending a few filaments to the trachea and to the pericardium.

7. The œsophageal branches, distributed to the lower third of the œsophagus.

8. The abdominal branches, the left distributed to the stomach and the liver; and the right, sending a few filaments to the stomach, and distributed finally to the liver,

spleen, kidneys, suprarenal capsules, and the whole of the small intestine.

The true filaments of origin of the pneumogastrics are exclusively sensory, and the nerves contain no motor filaments, except those derived from their anastomoses.

The sensory filaments of the auricular branches give sensibility to the upper part of the external auditory meatus and the membrana tympani.

The motor filaments of the pharyngeal branches animate the muscles of the pharynx. The sensory filaments are not important in the reflex phenomena of deglutition, but probably contribute slightly to the general sensibility of the pharynx.

The superior laryngeal nerves give sensibility to the upper portion of the larynx. They are exquisitely sensitive, and, by their reflex action, aid in closing the larynx to the entrance of foreign substances, and in the production of the movements of deglutition. Stimulation of these nerves produces movements of deglutition and arrests the action of the diaphragm. They animate, also, the movements of the crico-thyroid muscles.

The inferior laryngeals contain chiefly motor filaments. They embrace the filaments from the spinal accessories, which preside over phonation. They also contain motor filaments from other sources, which preside over the respiratory movements of the glottis. Their division abolishes vocal sounds, and, in young animals, causes death by suffocation, the glottis being closed in inspiration. Galvanization of their central ends, after division, generally produces movements of deglutition and arrest of the action of the diaphragm.

The action of the cardiac branches has been studied by experiments upon the pneumogastrics in the cervical region. Division of the pneumogastrics in the neck increases the number of pulsations of the heart. Galvanization of the peripheral ends, after division, arrests the heart's action in diastole, and galvanization of the central ends has no effect

on the circulation. The direct inhibitory action of the pneumogastrics operates through filaments derived from the spinal accessories. Galvanization of the "depressor-nerves" retards, or may arrest the pulsations of the heart, by reflex action. This occurs only when the central ends of the divided nerves are stimulated. Galvanization of the central ends of these nerves also diminishes the pressure of blood in the large vessels. This is due to reflex action through the splanchnic nerves, by which the vessels of the intestines are dilated. No such effect is produced when the splanchnic nerves have been divided. There is no entirely satisfactory explanation of the influence of the pneumogastrics on the heart.

The action of the pulmonary branches has been studied chiefly by observations on the pneumogastrics in the cervical region. Division of the pneumogastrics in this situation, in young animals, produces almost instant death by closure of the glottis in inspiration. In animals full-grown, death occurs in from two to five days, and the respiratory acts are very much diminished in frequency. When death occurs in this way, the lungs are found partially or completely "car nified." This is due to mechanical causes. The small pulmonary vessels are ruptured by the excessively deep inspirations, and blood is gradually effused and coagulates. The pneumogastrics have but little to do in conveying to the nerve-centres the sense of want of air which gives rise to the respiratory movements. Galvanization of the central ends of the pneumogastrics divided in the cervical region has the following effects: A very feeble excitation accelerates, and a more powerful excitation retards respiration. A sufficiently powerful excitation arrests respiration. Galvanization of the peripheral ends has no effect on respira tion.

The œsophageal branches supply only the lower third of the œsophagus. The upper portion receives branches from the inferior laryngeals, and the middle portion is supplied by branches from the posterior pulmonary nerves. The sen-

sibility of the mucous membrane of the œsophagus, as well as the movements of its muscular coat, depends upon these branches. Division of the nerves paralyzes the œsophagus, and galvanization of the roots of the pneumogastrics causes the tube to contract in its entire length. When the nerves are divided, the œsophagus may become distended with food forced in by the constrictors of the pharynx, but little or none passes to the stomach. Regurgitation of food sometimes occurs under these conditions, the muscular coat of the œsophagus contracting under the direct stimulus of distention.

The function of the abdominal branches has been studied chiefly by operating on the pneumogastrics in the cervical region. Division of the nerves produces congestion of the liver, and sometimes slight extravasation, and renders the bile somewhat watery. It also arrests, in from one to two days, the glycogenic function of the liver. Galvanization of the peripheral ends of the divided nerves has no effect on the liver. Galvanization of the central ends exaggerates the glycogenic function and renders animals diabetic. The inhalation of irritating vapors or of anæsthetics has the same effect. This action is reflex, and the direct stimulus to the liver does not pass through the pneumogastrics, for division of the nerves between the lungs and the liver has no influence on the production of sugar. Irritation of the floor of the fourth ventricle, opposite the origin of the pneumogastrics, exaggerates the glycogenic function. The stimulus is not propagated through the pneumogastrics, for the effect is the same after both nerves have been divided. It probably operates through the sympathetic, for diabetes cannot be produced after the branches going to the solar plexus have been divided.

Section of the pneumogastrics in the neck paralyzes, nearly but not entirely, the muscular coats of the stomach. When the section is made in an animal in full digestion, the mucous membrane, from being tense and full of blood, be

comes pale and flaccid, and stomach-digestion is arrested. Afterward, very feeble movements of the stomach may occur as the result of local irritation, and small quantities of food, very finely divided, may be digested. Galvanization of the nerves in the neck produces contractions of the muscular coats of the stomach. This action probably takes place through sympathetic filaments going to the pneumogastrics high up in the cervical region. Section of the nerves slightly retards absorption from the stomach.

After division of both pneumogastrics in the neck, purgative poisons, given even in fatal doses, generally fail to produce watery discharges from the intestine.[1]

[1] Compression of the pneumogastrics has lately been recommended by Waller to produce anæsthesia in surgical operations, etc. The effects of pressure of these nerves in the human subject are described by Aristotle, quoted by Waller. In some cases, the patient falls instantly, as if struck by lightning, while in others the effects are not so marked. Waller has employed this method for the production of anæsthesia under varied conditions, and has never observed any serious after-effects. He relates a case of successful reduction of a very difficult dislocation of the shoulder, which had resisted previous efforts, after two or three minutes of simultaneous compression and traction. He also relates a case of painless extraction of a tooth by the same means. The impossibility of compressing the pneumogastrics, in the human subject, without disturbing the circulation in the brain by pressure on the carotids, in view of the fact that cerebral anæmia produces anæsthesia, renders it impossible to accept, without reserve, the conclusions of Waller. (WALLER, *On the Compression of the Vagus Nerve, considered as a Means of producing Asthenia or Anæsthesia in Surgical Operations.—Practitioner*, London, December, 1870, No. xxx., p. 322.)

CHAPTER IX.

PHYSIOLOGICAL ANATOMY AND GENERAL PROPERTIES OF THE SPINAL CORD.

General arrangement of the cerebro-spinal axis—Membranes of the encephalon and spinal cord—Cephalo-rachidian fluid—Physiological anatomy of the spinal cord—Direction of the fibres after they have penetrated the cord by the roots of the spinal nerves—General properties of the spinal cord—Effects of stimulation applied directly to different portions of the cord.

Under the head of special senses, we shall consider, in another volume, the properties and functions of the first and second nerves, the portio mollis of the seventh, or auditory, and the gustatory nerves, comprising a part of the glosso-pharyngeal and a small filament from the facial (the chorda tympani) going to the lingual branch of the fifth. This will include a full account of the organs of smell, sight, hearing, and taste, with a description of the general sensory nerves, as far as they are concerned in the sense of touch. We will here begin our history of the cerebro-spinal axis, which will include the physiological anatomy, properties, and functions of the encephalon and spinal cord.

General Arrangement of the Cerebro-spinal Axis.—The nervous matter contained in the cavity of the cranium and in the spinal canal, exclusive of the roots of the cranial and spinal nerves, is known as the cerebro-spinal axis. This portion of the nervous system is composed of white and gray nervous matter. The fibres of the white matter act as conductors. The gray matter constitutes a chain of ganglia,

which act as nerve-centres, receiving impressions and generating the so-called nerve-force. The gray matter of the spinal cord also serves, to a greater or less extent, as a conductor.

The cerebro-spinal axis is enveloped in membranes, for its protection and for the support of its nutrient vessels. It is surrounded, to a certain extent, with liquid, and presents cavities, as the ventricles of the brain and the central canal of the cord, which contain liquid. The gray matter is distinct from the white, even to the naked eye. In the spinal cord, the white substance is external and the gray is internal. The surface of the brain presents an external layer of gray matter, the white substance being internal. In the white substance of the brain, also, we find collections of gray matter. As we should expect from the similarity in function between the white matter and the nerves, this portion of the cerebro-spinal axis is composed largely of fibres. The gray substance is composed chiefly of cells.

The encephalon is contained in the cranial cavity. In the human subject and in many of the higher animals, its surface is marked by numerous convolutions, by which the extent of its gray substance is very much increased. The cerebrum, the cerebellum, and all of the encephalic ganglia are connected with the white substance, and are continuous with the spinal cord. With the encephalon and the cord, all of the cerebro-spinal nerves are connected. The cerebro-spinal axis acts as a conductor, and its different collections of gray matter, or ganglia receive impressions conveyed by the sensory conducting fibres, and generate nerve-force, which is transmitted to the proper organs by the motor fibres.

Membranes of the Encephalon and Spinal Cord.—The membranes of the brain and spinal cord are, the dura mater, the arachnoid, and the pia mater.

The dura mater of the encephalon is a dense, fibrous

membrane, in two layers, composed chiefly of inelastic tissue, which lines the cranial cavity and is adherent to the bones. In certain situations, its two layers become separated and form what are known as the venous sinuses. The dura mater also sends off folds or processes of its internal layer; one of these passes into the longitudinal fissure, and is called the falx cerebri; another lies between the cerebrum and the cerebellum, and is called the tentorium; another is situated between the lateral halves of the cerebellum, and is called the falx cerebelli. The dura mater is closely attached to the bone at the border of the foramen magnum. From this point, it passes into the spinal canal and forms a loose covering for the cord. In the spinal canal, this membrane is not adherent to the bones, which have, like most other bones in the body, a special periosteum. At the foramina of exit of the cranial and the spinal nerves, the dura mater sends out processes which envelop the nerves, with the fibrous sheaths of which they soon become continuous.

The arachnoid is an excessively delicate serous membrane, in two layers, the surfaces of which are nearly in contact. The external layer lines the internal surface of the dura mater.[1] Like the other serous membranes, the arachnoid is covered with a layer of tessellated epithelium. There is a small amount of liquid between the two layers of the arachnoid; but by far the greatest quantity of liquid surrounding the cerebro-spinal axis lies beneath both layers, in what is called the subarachnoid space. This is called the cerebro-spinal, or cephalo-rachidian fluid. The fact that it exists in greatest quantity beneath both layers of the arachnoid was first pointed out by Magendie.[2] The arachnoid does not follow the convolutions and fissures of encephalon or the sulci of

[1] According to Kölliker, the arachnoid consists of a single layer, the layer attached to the dura mater being not properly a membrane, but simply an epithelial covering (*Handbuch der Gewebelehre*, Leipzig, 1867, S. 308).

[2] MAGENDIE, *Recherches physiologiques et cliniques sur le liquide céphalo-rachidien*, Paris, 1842.

the cord, but simply covers their surfaces. Magendie pointed out a longitudinal, incomplete, cribriform, fibrous septum in the cord, passing from the inner layer of the arachnoid to the pia mater. A similar arrangement is found in certain situations at the base of the skull.[1]

The pia mater of the encephalon is a delicate fibrous structure, exceedingly vascular, seeming to present, indeed, only a skeleton net-work of fibres for the support of the vessels going to the nervous substance. This membrane covers the surface of the encephalon immediately, follows the sulci and fissures, and is prolonged into the ventricles, where it forms the choroid plexus and the velum interpositum. From its internal surface, small vessels are given off which pass into the nervous substance.

The pia mater of the encephalon is continuous with the corresponding membrane of the cord ; but in the spinal canal, it is thicker, stronger, more closely adherent to the subjacent parts, and its blood-vessels are by no means so numerous. In this situation, many of the fibres are arranged in longitudinal bands. This membrane lines the anterior sulcus and a portion of the posterior sulcus. It is sometimes spoken of as the neurilemma of the cord.

At the foramina of exit of the cranial and the spinal nerves, the fibrous structure of the pia mater becomes continuous with the nerve-sheaths.

Between the anterior and posterior roots of the spinal nerves on either side of the cord, is a narrow ligamentous band, the ligamentum denticulatum, which assists in holding the cord in place. This extends from the foramen magnum to the terminal filament of the cord, and is attached, internally, to the pia mater, and externally, to the dura mater.

It is not necessary to enter into a detailed description of the arrangement of the blood-vessels, nerves, and lymphatics of the membranes of the brain and spinal cord, or of the vascular arrangement in the substance of the cerebro-spinal axis,

[1] MAGENDIE, *op. cit.*, p. 14.

as these points are chiefly of anatomical interest. The circulation in these parts presents certain peculiarities. In the first place, the encephalon being contained in an air-tight case of invariable capacity, it has been a question whether or not the vessels be capable of contraction and dilatation, or whether the quantity of blood in the brain be subject to modification in health or disease. This question may certainly be answered in the affirmative. In infancy and in the adult, when an opening has been made in the skull, the volume of the encephalon is evidently increased during expiration and is diminished in inspiration. Under normal conditions, in the adult, it is probable that the amount of blood is increased in expiration and diminished in inspiration; but it is not probable that the cerebro-spinal axis undergoes any considerable movements. The important peculiarities in the cerebral circulation have already been fully considered in another volume.[1]

An important fact was pointed out by Robin, and afterward by His, with regard to the arrangement of the lymphatic vessels of the brain. It was shown by these observers, that the encephalic capillaries are surrounded or nearly surrounded by canals (perivascular canal-system) which exceed the blood-vessels in diameter by from $\frac{1}{1200}$ to $\frac{1}{400}$ of an inch, and are connected with lymphatic trunks or reservoirs situated under the pia mater.[2] The system of canals may, by variations in its contents, serve to equalize the amount of liquid in the brain as its blood-vessels are distended or contracted.

Cephalo-rachidian Fluid.—The older writers referred to in works upon physiology, as giving the most accurate description of the cephalo-rachidian fluid, are Haller[3] and Cotugno;[4] but it remained for Magendie, in 1825, to de-

[1] See vol. i., Circulation, p. 332. [2] See vol. ii., Absorption, p. 433.

[3] HALLER, *Elementa Physiologiæ*, Lausannæ, 1762, tomus iv., p. 87.

[4] *Extrait de la dissertation de* COTUGNO, *de Ischiade Nervosa, contenue dans le*

scribe its exact situation, with the communications between the different cavities of the brain and the subarachnoid space.[1] By a series of ingeniously-contrived experiments upon the cadaver and in living animals, Magendie showed that the greater part of the fluid in the cranium and the spinal canal is contained in what is known as the subarachnoid space; that is, between the inner layer of the arachnoid and the pia mater, and not between the two layers of the arachnoid. The ventricles of the encephalon are in communication with the central canal of the cord, and, as was shown by Magendie, they are also in communication with the general subarachnoid space, by a narrow, triangular orifice, situated at the inferior angle of the fourth ventricle. By this arrangement, the liquid in the ventricles of the encephalon and the central canal of the cord communicates with the liquid surrounding the cerebro-spinal axis, and the pressure upon these delicate parts is equalized.

As far as we know, the function of the cephalo-rachidian fluid is simply mechanical, and its properties and composition have no very definite physiological significance. Its quantity was estimated by Magendie at about two fluidounces;[2] but this was the smallest amount obtained by placing the subject upright, making an opening in the lumbar region and a counter-opening in the head to admit the pressure of the atmosphere. The exact quantity in the living subject could hardly be estimated in this way; and it is difficult, indeed, to see how any thing more than a roughly approximative idea could be obtained. The quantity obtained by Magendie probably does not represent the entire amount of liquid contained in the ventricles and in the sub-

Thesaurus Dissertationum de SANDIFERT, tome ii., p. 411, Roterdam, 1769.—*Journal de physiologie*, Paris, 1827, tome vii., p. 83.

[1] MAGENDIE, *Mémoire sur un liquide qui se trouve dans le crane et le canal vertébral de l'homme et des animaux mammifères.—Journal de physiologie*, Paris, 1825, tome v., p. 27; Ibid., 1827, tome vii., pp. 1, 66; and, *Recherches physiologiques et cliniques sur le liquide céphalo-rachidien*, Paris, 1842.

[2] MAGENDIE, *Liquide céphalo-rachidien*, Paris, 1842, p. 36.

arachnoid space, but it is the most definite estimate that has been given.

The discharge of a certain quantity of the cephalo-rachidian fluid does not produce any marked derangement in the action of the nervous system. In the first experiments of Magendie, in which the muscles of the neck and the occipito-atloid ligament were divided, the animals were affected with irregular movements, general paralysis, etc.;[1] but it is stated by Longet[2] and by Bernard, that these phenomena are due to the division of the parts involved in the operation, and not to the removal of the liquid. When the liquid is allowed to flow spontaneously through a small trocar introduced without division of the muscles of the neck, there follows no serious nervous disturbance; but when the liquid is drawn out forcibly with a syringe, the animal first becomes enfeebled, and afterward seems affected with general paralysis. These phenomena are attributed by Bernard, not so much to removal of the fluid, as to congestion of blood-vessels and even effusion of blood, which follow sudden diminution in the pressure.[3]

Sudden increase in the quantity of liquid surrounding the cerebro-spinal axis produces coma, probably from compression of the centres. This was shown by Magendie, by injecting water in animals, and also by compressing the tumor, in cases of spina bifida in the human subject, by which the fluid was pressed back into the spinal canal. In the cases of spina bifida, the subject, during the compression, fell into coma, which was instantly relieved by removing the pressure.[4]

It was ascertained by Magendie, and this has been confirmed by all later observers, that the cephalo-rachidian fluid

[1] MAGENDIE, *Liquide céphalo-rachidien*, Paris, 1842, p. 58.

[2] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 305.

[3] BERNARD, *Système nerveux*, Paris, 1858, tome i., p. 496, *et seq.*

Bernard states that Magendie recognized the error in his first interpretation of the phenomena following removal of the cephalo-rachidian fluid (Ibid., p. 496).

[4] MAGENDIE, *op. cit.*, p. 60.

is speedily reproduced after its evacuation. In all probability, it is secreted by the pia mater.[1]

The general properties and composition of the fluid under consideration are, in brief, the following:[2] It is perfectly transparent and colorless, free from viscidity, of a distinctly saline taste, alkaline reaction, and resists putrefaction for a long time. It is not affected by heat or acids. As we should expect from its low specific gravity and purely mechanical function, it contains a large proportion of water; 981 to 985 parts per thousand. It contains a considerable quantity of chloride of sodium, a trace of chloride of potassium, sulphates, carbonates, and alkaline and earthy phosphates. In addition, it contains traces of urea, glucose, lactate of soda, fatty matter, cholesterine, and albumen.

As a summary of the function of the cephalo-rachidian fluid, it may be stated, in general terms, that it serves to protect the cerebro-spinal axis, chiefly by equalization of the pressure in the varying condition of the blood-vessels, accurately filling the space between the centres and the bony cavities in which they are contained. That the blood-vessels of the cerebro-spinal axis are subject to variations in tension, is readily shown by introducing a canula into the subarachnoid space, when the jet of fluid discharged will be increased with every violent muscular effort.[3] The pressure of the fluid, in this instance, could only be affected through the blood-vessels.

Physiological Anatomy of the Spinal Cord.

The spinal cord, with its membranes, the roots of the spinal nerves, and the surrounding liquid, occupies the spinal canal and is continuous with the encephalon. Its length is from fifteen to eighteen inches, and its weight is about an ounce and a half. Its form is cylindrical, slightly flat-

[1] *Op. cit.*, pp. 38, 39.

[2] Robin, *Leçons sur les humeurs*, Paris, 1867, p. 259.

[3] Magendie, *Journal de physiologie*, Paris, 1827, tome vii., p. 9.

tened in certain portions. It extends from the foramen magnum to the first lumbar vertebra. It presents, at the origin of the brachial nerves, an elongated enlargement, and a corresponding enlargement at the origin of the nerves which supply the lower extremities. It terminates below in a slender, gray filament, called the filum terminale. The sacral and coccygeal nerves, after their origin from the lower portion of the cord, pass downward to emerge by the sacral foramina, and form what is known as the cauda equina.

The substance of the cord is formed of white and gray matter, the white matter being external. The proportion of white matter to the gray is greatest in the cervical region. This fact is important in studying the course of the fibres and in view of the functions of the cord as a conductor. The inferior, pointed termination of the cord consists entirely of gray matter.

The cord is marked by an anterior and a posterior median fissure, and by imperfect and somewhat indistinct anterior and posterior lateral grooves, from which arise the anterior and the posterior roots of the spinal nerves. The posterior lateral groove is tolerably well marked, but there is no distinct line at the origin of the anterior roots. The anterior median fissure, or sulcus, is perfectly distinct. It penetrates the anterior portion of the cord in the median line for about one-third of its thickness, and receives a highly-vascular fold of the pia mater. It extends to the anterior white commissure. The posterior fissure is not so distinct as the anterior, and is not lined throughout by a fold of the pia mater, but is filled with connective tissue and blood-vessels, which form a septum posteriorly, between the lateral halves of the cord. The posterior median fissure, so called, extends nearly to the centre of the cord, to the posterior gray commissure.

Physiologically and anatomically, the cord is divided into two lateral halves; but the division of each half into columns is not so distinct. Anatomists generally regard a

half of the cord as consisting of three columns: The anterior column is bounded by the anterior fissure and the origin of the anterior roots of the spinal nerves; the lateral column is included between the anterior and the posterior roots of the nerves; the posterior column is bounded by the line of origin of the posterior roots and the posterior fissure. Some anatomists include the lateral with the anterior column, under the name of the antero-lateral column, taking in about two-thirds of the cord. Next the posterior median fissure, is a narrow band, marked by a faint line, which is sometimes called the posterior median column.

The arrangement of the white and the gray matter in the cord is seen in a transverse section. The gray substance is in the form of a letter H, presenting two anterior and two posterior cornua connected by what is called the gray commissure. The anterior cornua are the shorter and broader, and do not reach to the surface of the cord. The posterior cornua are larger and narrow, and extend nearly to the surface, at the point of origin of the posterior roots of the spinal nerves. In the centre of the gray commissure, is a very narrow canal, lined by cells of ciliated epithelium, called the central canal. This is in communication above with the fourth ventricle, and extends below to the filum terminale. That portion of the gray commissure in front of this canal is sometimes called the anterior gray commissure, the posterior portion being known as the posterior gray commissure. The central canal is immediately surrounded by connective tissue. In front of the gray commissure, is a mass of white substance known as the anterior white commissure.

The proportion of the white to the gray substance is variable in different portions of the cord. In the cervical region, the white substance is most abundant, and, in fact, it progressively increases in quantity from below upward throughout the whole extent of the cord. In the dorsal region, the gray matter is least abundant, and it exists in greatest quantity in the lumbar enlargement.

The white substance of the cord is composed of nerve-fibres, connective-tissue elements, and blood-vessels, the latter arranged in a very wide and delicate plexus. The nerve-fibres are variable in their size, and are composed of the axis-cylinder surrounded by the medullary substance, without, however, the investing membrane. We will speak farther on of the direction of the fibres in the cord.

The anterior cornua of gray matter contain blood-vessels, connective-tissue elements, very fine nerve-fibres, and large multipolar nerve-cells, which are sometimes called motor cells. The posterior cornua are composed of the same elements, the cells being much smaller, and the fibres exceedingly small, presenting very fine plexuses. The cells in this situation are sometimes called sensory cells. Near the posterior portion of each posterior cornu, is an enlargement, of a gelatiniform appearance, containing numerous small cells and fibres, called the substantia gelatinosa.

The foregoing description of the different structures and parts of the cord is necessary to a comprehension of the direction of the fibres in the spinal axis and their connections with the nerve-cells, which is the anatomical basis of our knowledge of its physiology. The connections between the cells and the fibres have already been described in the chapter on the general structure of the nervous system.[1] The multipolar nerve-cells are supposed to present certain prolongations which do not branch and are directly connected with the medullated nerve-fibres. These are called nerve-prolongations. In addition, fine, branching poles are described under the name of protoplasmic prolongations.

The direction of the fibres in the cord is one of the most difficult and complicated questions in physiological anatomy; and, especially as regards the posterior roots of the nerves, is one which cannot as yet be elucidated by purely anatomical investigations, but requires the aid of experimental and pathological observations.

[1] See page 50.

Direction of the Fibres after they have penetrated the Cord by the Roots of the Spinal Nerves.—In order to understand fully the importance of this question, it is necessary to bear in mind the following physiological facts:

1. The cord serves as a conductor of impressions to the brain, conveyed to it through the posterior roots, and of stimulus generated by the brain and passing from the cord by the anterior roots of the spinal nerves. This action is crossed, the decussation taking place mainly at the medulla oblongata, for the anterior portions, and throughout the whole extent of the cord, for the posterior portions.

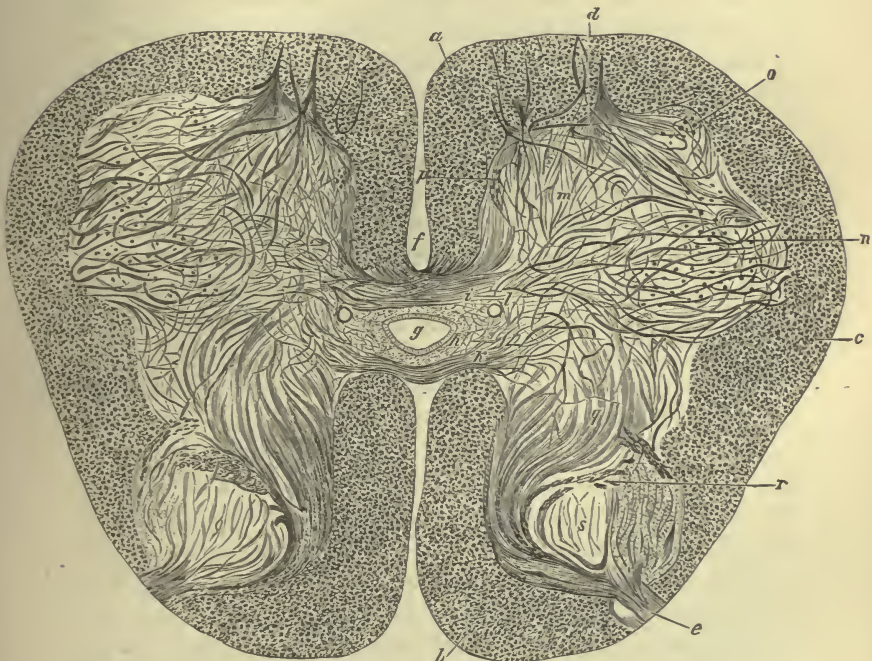
2. Independently of its action as a conductor, the cord, disconnected from the rest of the cerebro-spinal axis, acts as a nerve-centre, by virtue of its gray matter and the fibres connected with the cellular elements of this substance.

Bearing in mind these points, which are matters of positive demonstration, we are prepared to study the anatomical relations of the fibres and cells. In this, we cannot follow minutely and critically discuss the elaborate investigations of Stilling, Clarke, Kölliker, Van der Kolk, Gerlach, Dean, and others, without treating extensively of points which possess a purely anatomical and a more or less controversial interest; and we will content ourselves with the following very recent description, quoted in full from Gerlach, which embodies about all of our positive knowledge of the subject, presented in the clearest manner possible. This extract, the translation of which is almost literal, should be carefully studied by those who desire to learn what is known at the present day with regard to the physiological anatomy of the cord. As a preparation for this study, it would be well to closely examine Fig. 10, which gives a general view of the different parts of the cord, shown in a transverse section:

"With the present methods and means of investigation at our command, we can scarcely give an exact, detailed description of the course of the fibres in the spinal cord, the ground-work of the physiology of this organ. Investigations

up to this time afford at least the outlines of a sketch which, as regards the course of the fasciculi of the anterior roots, has a tolerably definite basis; and, on the other hand, with

Fig. 10.



Transverse section of the spinal cord of a child six months old, at the middle of the lumbar enlargement, treated with potassio-chloride of gold and nitrate of uranium By means of these reagents, the direction of the fibres in the gray substance is rendered unusually distinct. Magnified 20 diameters.—*a*, anterior columns; *b*, posterior columns; *c*, lateral columns; *d*, anterior roots; *e*, posterior roots; *f*, anterior white commissure, in communication with the fasciculi of the anterior cornua and the anterior columns; *g*, central canal with its epithelium; *h*, surrounding connective substance of the central canal; *i*, transverse fasciculi of the gray commissure in front of the central canal; *k*, transverse fasciculi of the gray commissure behind the central canal; *l*, transverse section of the two central veins; *m*, anterior cornua; *n*, great lateral cellular layer of the anterior cornua; *o*, lesser anterior cellular layer; *p*, smallest, median cellular layer; *q*, posterior cornua; *r*, ascending fasciculi in the posterior cornua; *s*, substantia gelatinosa (Gerlach, in Stricker, *Handbuch der Lehre von den Geweben*, Leipzig, 1868, S. 666).

regard to the fasciculi going to the spinal cord through the posterior roots, is quite incomplete and uncertain.

"The fasciculi of the anterior roots, after their entrance into the cord, pass diagonally through the white substance,

and, as such, are not at all concerned in its formation. On the contrary, they pass immediately to the gray substance of the anterior cornua, and, by their prolongations, are in direct connection with the nerve-cells in this situation, which, accordingly, are to be regarded as the elements of origin of the anterior roots in the cord. The protoplasmic processes of these nerve-cells form parts of the fine plexuses of nerve-fibres in the gray substance, from which larger nerve-fibres take their origin. These, extending in two directions, leave the gray substance, to pass up in the white substance to the brain. In consequence of the entrance of additional nerve-fibres, the white substance is necessarily increased in quantity in the cord from below upward. With regard to the course of the fasciculi which pass out of the gray substance of the anterior cornua, these are to be divided into median and lateral. The median fasciculi pass immediately into the anterior white commissure, where they decussate with corresponding fasciculi from the opposite side, to pass upward again in the anterior column of the other half of the cord. The lateral fasciculi go to the lateral columns of the same side, in which they pass to the brain, having first undergone decussation in the anterior pyramids of the medulla oblongata.

"The posterior nerve-roots enter horizontally, running in the white substance of the spinal cord, in a direction from without inward toward the median line, and here divide into two portions. The lateral portion, the smaller, retains the horizontal direction, and passes through the substantia gelatinosa, dividing into fine and the finest bundles, in the manner mentioned above, to take part in the formation of the vertical bundle of fibres which lie immediately in front. Here the fibres pass onward, a portion of them ascending and a portion descending. The fibres of the lateral portion of the posterior roots do not remain very long in the vertical bundle, but curve forward in an horizontal plane, and in this way reach the portion of the posterior cornua containing a fine plexus of nerve-fibres.

"The median (larger) portion of the posterior root-fibres passes to that portion of the posterior column which bounds the substantia gelatinosa internally and posteriorly; and curving, takes here a vertical course to pass into the posterior columns, extending chiefly upward, but perhaps downward as well. The median posterior root-fibres then undergo another deflection, by which they again take an horizontal direction, and pass to the gray substance of the posterior cornua, in part through the median portion and in part by the inner border of the substantia gelatinosa. With regard to the further course of the posterior root-fibres, it is impossible to present positive explanations, for the reason that the present methods of investigation do not afford any means of distinguishing the posterior fibres from the nerve-tubes in the vertical fasciculi of the posterior cornua, or those passing from the gray substance into the posterior columns, to ascend to the brain. The numerous divisions which the posterior root-fibres penetrating the posterior cornua immediately undergo indicate, however, that a portion of them is lost directly in the fine nerve-plexus of the gray substance. But at the same time there are numerous fibres which extend forward, and others which take a more or less wavy course toward the median line. The first, perhaps, can be regarded as posterior root-fibres, which pass in a forward direction in the nervous plexus; the latter, on the other hand, belong to the commissural fibres, which cross the median line in the gray substance in front of and behind the central canal. In my opinion, the fibres which penetrate the posterior commissure are not to be regarded as belonging directly to the posterior roots, but are to be considered as fibres which pass backward to go either to the vertical fasciculi of the gray substance, or to pass to the brain in the posterior columns. If this idea be correct, and it is sustained by analogous conditions in the anterior cornua, the following view may be given of the course of the fibres of the posterior roots which penetrate the gray substance: 'A portion of the posterior

root-fibres, immediately after their entrance into that portion of the gray substance which contains a nerve-plexus, is lost in this plexus; another portion extends farther forward, and, in proportion as the fibres pass forward, they likewise take part, by constant divisions, in the formation of the nerve-plexus. This plexus, in which larger and smaller nerve-cells are interspersed as it were as knotted points (*Knotenpunkte*), are in direct connection with the plexus of the anterior cornua. From these cells nerve-fibres arise, which cross the median line in the gray commissure in front of and behind the central canal, then curve backward, to pass up to the brain, in part in the vertical fasciculi of the posterior cornua, in part in the posterior columns, between both of which numerous connections may exist which are as yet inextricable.' This view involves a complete decussation in the spinal cord, through the fibrous elements of the posterior roots passing into this part. Whether this be in reality a complete or a partial decussation in this situation, a part of the fibres arising from the nerve-plexus passing simply backward without crossing the median line, cannot be determined by definite anatomical investigations; but pathological researches, as well as the experimental results of that most competent observer, Brown-Séquard, are decidedly in favor of a complete decussation.

"Finally, it must be admitted that two points especially are evident:

"1. In the direction of the nerve-fibres which enter through the posterior roots, the gray substance has more numerous connections than in those which pass to the spinal cord through the anterior roots.

"2. The morphological distinction determinable between the anterior and the posterior roots is, that the former take their origin directly from the nerve-cells by means of the nerve-prolongations, while in the latter, it is only indirect through the nerve-plexus with the protoplasmic prolonga-

tions, and in this wise they are in communication with the nerve-cells." [1]

General Properties of the Spinal Cord.

In treating of the functions of the spinal cord, we shall consider, first, its general properties, as shown by direct stimulation of its substance in different situations; next, its functions as a conductor; and, finally, its action as a nerve-centre.

The first indication that the different columns of the cord are possessed of different properties is to be found in the experiments of Magendie. This observer, however, was somewhat indefinite in his conclusions, particularly with regard to the anterior columns; but he stated distinctly that the posterior columns are sensitive: "If we lay bare the cord in any portion of its extent, and if we touch, or prick slightly posteriorly, the two fasciculi situated between the posterior roots, the animal gives signs of exquisite sensibility; if, on the other hand, we make the same trials upon the anterior portion, the evidences of sensibility are scarcely apparent." [2] Since this time, numerous observers have experimented upon the different columns, both at the surface and in the deep portions of the cord, with varying results. These observations we do not propose to discuss fully in detail, but will refer simply to certain of them, made within a few years, with the advantage of a knowledge of the reflex phenomena following irritation of the cord, which must always be taken into consideration in such experiments.

In 1861, Chauveau, as the result of numerous experiments performed upon horses, cows, sheep, goats, rabbits, pigs, dogs, and cats, stated that the antero-lateral columns of the cord were inexcitable, both at the surface and in the

[1] GERLACH, in STRICKER, *Handbuch der Lehre von den Geweben*, Leipzig, 1868, S. 691, *et seq.*

[2] MAGENDIE, *Note sur le siége du mouvement et du sentiment dans la moelle épinère.—Journal de physiologie*, Paris, 1823, tome iii., p. 153.

deep portions. The facts upon which this assertion was based were, that direct stimulation of these portions of the cord in living animals, whether by mechanical means or by feeble galvanic shocks, produced no contraction of muscles and no pain. Upon irritating the posterior columns, either by mechanical or galvanic stimulus, Chauveau noted pain and reflex movements when the irritation was applied to the surface, but the results were negative when the deep portions of the columns were operated upon. The surface of the posterior columns seemed to possess the same general properties as the posterior roots of the nerves, especially near the roots, where the sensibility was most marked, gradually diminishing in intensity toward the median line; but the deep portions of the cord were everywhere found completely insensible and inexcitable.[1]

The experiments and conclusions of Chauveau have a most important bearing upon the physiology of the cord, and are opposed to the views of the majority of physiological writers, though they have been admitted by some experimenters. We shall discuss first the experiments upon the antero-lateral columns, which are most remarkable in their negative results. In this we shall use the term excitability as signifying the property of the cord which enables it to conduct a stimulus applied directly to it to certain muscles, producing convulsive movements confined to these muscles, and not of a reflex character. We shall apply the term sensibility to the property by virtue of which an irritation directly applied is conveyed to the brain and produces a painful impression.

The experiments of Chauveau and some others upon the antero-lateral columns are simply negative; but their results are directly opposed to those of numerous experimenters, who have produced local and restricted convulsive movements by direct irritation of both the superficial and the

[1] CHAUVEAU, *De l'excitabilité de la moelle épinère.—Journal de la physiologie*, Paris, 1861, tome iv., p. 369.

deep portions of these columns. The experiments of Longet, for example, made in 1840, have been repeatedly confirmed by more recent observations. Longet exposed the lumbar portion of the cord in a large-sized dog and divided it transversely. Galvanization of the antero-lateral columns of the inferior portion always produced convulsive movements, while the result of irritation of the posterior columns was simply negative. On the other hand, galvanization of the posterior columns of the superior segment of the cord produced intense pain, and no effect followed irritation of the antero-lateral columns.[1] These results, being positive, are to be accepted in opposition to the negative results obtained by Chauveau, provided it can be shown that the stimulus did not extend from the cord to the roots of the nerves, a reservation which is important in all experiments in which the nerves are irritated with galvanism. Upon this point, we have some experiments, made in 1863, which will be detailed after we have discussed the properties of the posterior columns.

With regard to the posterior columns, the views of Chauveau are in advance of those of previous observers, only in so far as he has shown that, although the surface of this portion of the cord is endowed with sensibility, its deeper portions are entirely insensible, except in the immediate proximity of the posterior roots of the nerves.

In view of the importance of the question under consideration, and of the contradictory results of experiments, we repeated, in 1863, the experiments of Chauveau, under conditions as nearly physiological as possible. We had often had occasion to note the diminished sensibility of the roots of the spinal nerves immediately following the very severe operation of opening the spinal canal, and had also noted that the sensibility increased, probably approaching the normal standard, after the animal had been allowed a few hours

[1] LONGET, *Anatomie et physiologie du système nerveux*, Paris, 1842, tome i., p. 272, *et seq.*

of repose. For this reason, we made our observation about two hours after the first operation. To avoid the suspicion of an extension of the galvanic current beyond the portion of the cord which we desired to stimulate, the irritation was first made by simply scratching the parts with the point of a needle. The following experiment is the type of several, in all of which the results were identical:

May 28, 1863, at 1 P. M., the laminæ and the spinous processes of the three lower lumbar vertebræ were removed from a medium-sized dog. There was no very great hæmorrhage. The spinal cord and the roots of three of the nerves were exposed, and the wound was then closed. The operation was performed with the animal under the influence of ether, and lasted about three-quarters of an hour.

About two hours after the first operation, the animal was brought before the class at the Long Island College Hospital. The wound was opened, and the properties of the anterior and posterior roots were demonstrated. The following observations were then made on the spinal cord:

The external surface of the posterior columns was irritated by scratching with the point of a needle. This produced pain, the more marked, the nearer the irritation was brought to the origin of the posterior roots. The surface was almost insensible at the median line. A feeble galvanic stimulus was then applied by means of a *pince électrique*, with the same results. The deep portions of the posterior columns were then irritated without effect.

The cord was then divided transversely, and mechanical and galvanic stimulus were applied to the cut surfaces.

The surface of the upper end of the cord was irritated with the needle, and the needle was plunged deeply into its substance, without effect. The same negative results followed application of the galvanic stimulus.

The lower end of the cord was then elevated with a hook, and the surface of the anterior columns was irritated by the needle and by galvanism. The invariable effect was con-

vulsive movements in the lower extremities, without pain. The same irritation was applied to the deep portions of the anterior columns with like results; *i. e.*, convulsive movements in the lower extremities, following the irritation immediately.

The above-mentioned phenomena were fully verified by repeated experiments, and the animal was then killed by section of the medulla oblongata.

The general movements accompanied by evidences of pain were readily distinguishable from the local convulsive movements with no pain.

This experiment fully confirms the observations of Chauveau with regard to the posterior columns, but shows, in opposition to Chauveau, that the anterior columns are excitable, both at the surface and in the deep portions. The recent observations of Vulpian are also opposed to the results obtained by Chauveau with regard to the antero-lateral columns. From a number of carefully-executed experiments, Vulpian draws the following conclusions:

"1. The gray substance is absolutely inexcitable.

"2. The anterior fasciculi possess a certain degree of motor excitability.

"3. There is no doubt that the posterior fasciculi are very excitable. They are sensitive and excito-motor if the cord be left intact, and simply excito-motor if the cord be divided transversely and separated from the encephalon. It is the same, but to a less degree, in that portion of the lateral fasciculi contiguous to the posterior fasciculi." [1]

In the face of definite and positive experiments showing the excitability of certain portions of the cord, it is impossible to accept the purely negative results obtained by Chauveau and others. This remark applies to recent experiments made by Huizinga, carrying out the observations of Van Deen, in which he assumes to show that the anterior

[1] VULPIAN, *Leçons sur la physiologie générale et comparée du système nerveux*, Paris, 1866, p. 362.

columns are not excitable, even near the roots of the nerves; and that when convulsive movements follow galvanization near the roots, this is due to an extension of the current to the roots themselves.[1]

As the result of the most definite and reliable experiments of others, bearing upon the question of the properties of the cord, and of our own observations, we have arrived at the following conclusions:

The gray substance is probably inexcitable and insensible under direct stimulation.

The antero-lateral columns are insensible, but are excitable both on the surface and in their substance; *i. e.*, direct stimulation will produce convulsive movements in certain muscles, which movements are not reflex and are not attended with pain. The lateral columns are less excitable than the anterior columns.

The surface, at least, of the posterior columns is very sensitive, especially near the posterior roots of the nerves. The deep portions of the posterior columns are probably insensible, except very near the origin of the nerves.

The above conclusions refer only to the general properties of different portions of the cord, as shown by direct stimulation, in the same way that we demonstrate the general properties of the nerves in their course. In all probability, the fibres in the white and gray substance of the central nervous system conduct motor stimulus from the brain and sensory impressions to the brain, while they are themselves insensible and inexcitable under direct stimulation. The physiological action of the cord as a conductor, one of the most interesting and important of its functions, will be fully considered in another chapter.

[1] Huizinga, *Die Unerregbarkeit der vorderen Rückenmarkstränge.—Archiv für die gesammte Physiologie*, Bonn, 1870, Bd. iii., S. 81, *et seq.*

CHAPTER X.

ACTION OF THE SPINAL CORD AS A CONDUCTOR.

Transmission of motor stimulus in the cord—Decussation of the motor conductors of the cord—Decussation at the medulla oblongata—Decussation of the motor conductors in the cervical portion of the cord—Transmission of sensory impressions in the cord—The white substance of the posterior columns does not conduct sensory impressions—Action of the gray matter as a conductor—Probable function of the cord in connection with muscular coördination—Decussation of the sensory conductors of the cord—Summary of the action of the cord as a conductor.

In treating of the functions of the spinal cord, both as a conductor and as a nerve-centre, we shall endeavor to discuss those facts only which are, it is to be hoped, either definitively settled, or are in accordance with what is at present known in anatomy, physiology, and pathology. The literature upon this portion of our subject is so extended and diffuse, that a full, critical analysis of the different experiments and views that have been presented since the observations of Magendie, in 1823, would inevitably complicate and confuse our description. We shall give citations, however, which will enable the reader to refer readily to the most reliable historical and controversial discussions upon this subject.[1]

[1] Longet, in his treatise on physiology, gives a tolerably complete historical account of the numerous experimental researches concerning the functions of the cord as a conductor (*Traité de physiologie*, Paris, 1869, tome iii., p. 338, *et seq.*). The writings upon this subject by Brown-Séquard are very voluminous, and are scattered through numerous periodical publications, while many of his papers are controversial, and are reiterations of experiments and views previously pub-

Transmission of Motor Stimulus in the Cord.—The antero-lateral columns of the cord, both the white and the gray substance, are entirely insensible to direct irritation, and conduct the motor stimulus from the centres to the periphery. This statement may be accepted, as the result of positive demonstration, with very little qualification.

If the posterior columns of the cord be divided or even removed for a certain length, the animal retains the power of voluntary motion intact. It is supposed by Dr. Brown-Séquard that the white substance of the antero-lateral columns, in addition to its motor properties, takes a slight but well-defined part in the transmission of sensory impressions, and this idea is based upon experiments which seem to show that slight sensibility remains in the lower extremities after section of the posterior columns.[1] Such experiments, however, must be accepted with a certain degree of reserve, in view of the great difficulty of dividing the columns separately. If the white substance of the antero-lateral columns take any part in the conduction of sensory impressions, it is slight and unimportant. On the other hand, if the antero-lateral columns of the cord be divided on both sides, the power of voluntary motion is lost absolutely in all parts supplied with nerves coming from the cord below the section.

It would be an interesting point to determine positively the relative importance of the white and the gray substance of the anterior columns in the transmission of motor stimulus; but this has thus far been impossible. We cannot with certainty divide the gray matter of the anterior columns completely and leave the white substance intact, nor can we divide the white substance without injuring the gray. As far as experiments go, however, they seem to show that

lished. A list of his most important memoirs, with a short account of his experiments and conclusions, is given in the *Journal de la physiologie*, Paris, 1862, tome v., p. 641, *et seq.*

[1] Brown-Séquard, *Expériences montrant que les cordons antérieurs de la moelle épinère servent à la transmission des impressions sensitives.—Journal de la physiologie*, Paris, 1858, tome i., p. 809.

transmission is not effected exclusively by the white substance, but that the gray matter plays an important part in this function.[1] We shall refer, farther on, to the action of the gray substance in the transmission of sensory impressions.

It is evident, from anatomical facts as well as from the results of direct experimentation, that the fibres of conduction of motor stimulus pass from the brain to the anterior roots of the nerves, through the spinal cord, from above downward, and that there is no other medium for the transmission of the will to the muscles. Wherever the cord be divided, all the muscles supplied by nerves given off below the section are paralyzed. From the brachial enlargement of the cord, nerves of motion pass to the superior extremities, and the inferior extremities are supplied mainly by nerves coming from the lumbar enlargement. The direction of these motor fibres in the cord itself has only been elucidated by experiments upon living animals. If the anterior columns alone be divided in the dorsal region, there is almost complete paralysis of the lower extremities. If the lateral columns be divided in this situation, without injuring the anterior columns, voluntary movements of the lower extremities are diminished, but are not abolished. If the anterior columns be divided high up in the cervical region, there is a diminution in the voluntary movements, but by no means so marked as when the section is made in the dorsal region; but if the lateral columns be divided in the upper cervical region, the paralysis is almost or quite complete.[2]

The experiments just cited clearly show that the situation of the chief motor conductors of the cord is different in the dorsal and in the cervical region. In the dorsal region, while conduction of the motor stimulus takes place through fibres contained both in the anterior and in the lateral

[1] VULPIAN, *Leçons sur la physiologie générale et comparée du système nerveux*, Paris, 1866, p. 369.

[2] BROWN-SÉQUARD, *Physiology and Pathology of the Central Nervous System*, Philadelphia, 1860, p. 46. VULPIAN, *Système nerveux*, Paris, 1866, p. 370.

columns, the transmission is mainly through the anterior columns, the lateral columns being much less important. In the cervical region, the conditions are reversed, and the conduction takes place chiefly by means of the lateral columns. Passing from above downward, therefore, the motor fibres are situated in the cervical region mainly in the lateral columns; but progressively, as they pass through the dorsal and the lumbar portions of the cord, these fibres change their location and are found chiefly in the anterior columns.

Recent observations have not sustained the old idea that the lateral columns of the cord contain fibres which preside specially over the movements of the thorax. The experiments of Vulpian upon this point are conclusive. If the lateral column be divided on one side at about the third or fourth cervical vertebra, there is considerable enfeeblement of the muscles of the thorax upon the corresponding side, but there is also partial loss of power in the limbs, which is more marked in the anterior extremity. This diminution in power in the thoracic muscles is such, that in ordinary tranquil respiration, the side corresponding to the section does not move; but in difficult respiration, or in crying, the movements are very marked.

Decussation of the Motor Conductors of the Cord.—Well-established anatomical and pathological facts show conclusively that there is a complete decussation of the motor conductors of the cord; so that the stimulus of volition generated in one lateral half of the brain always passes to the opposite half of the body. If a lesion occur in the brain upon one side, so as to produce total paralysis of motion, the opposite side of the body is paralyzed, while voluntary motion is absolutely intact on the side corresponding to the injury. In the anterior pyramids of the medulla oblongata,

[1] Vulpian, *Système nerveux*, Paris, 1866, p. 371.

the decussation of the fibres is easily demonstrated anatomically. In view of these facts, concerning which there is no difference of opinion, it only remains to show by physiological experiments that decussation actually takes place at the medulla oblongata, and to submit to the same method of inquiry the following important question: Assuming that crossing of motor fibres takes place at the medulla, is this the sole seat of decussation of these fibres, or does it also exist in certain portions of the cord below?

The question of decussation at the medulla oblongata is easily answered. In the first place, we have the crossed action in hemiplegia and the easy anatomical demonstration of the decussating fibres. The experimental confirmation of these facts is not so simple, for the reason that animals survive operations upon the medulla oblongata for a very short time. As far as can be learned, however, from the latter mode of inquiry, the conclusions drawn from anatomy and pathology are fully sustained. If the medulla be exposed in a living animal, and "if a section is made longitudinally just at the place of the decussation of the anterior pyramids, so as to divide completely all of the decussating elements, we find that, although the animal lives some time after the operation, it has no voluntary movement at all in any of the limbs, which are almost always the seat of convulsions."[1]

The question of decussation of motor fibres in the cord itself is one which can be settled only by physiological experiments, as the course of the decussating fibres, if they exist, cannot be demonstrated anatomically. It is remarkable that Galen submitted this point to experimental investigation, by dividing the cord longitudinally in the median line in the lumbar region. This operation was not followed by loss of voluntary power in the lower extremities, showing that the motor fibres do not cross the median line, at

[1] Brown-Séquard, *Physiology and Pathology of the Central Nervous System*, Philadelphia, 1860, p. 49.

least in this portion of the cord.[1] Recent experiments upon the cervical portions of the cord show that there is a very slight decussation of motor fibres in this situation. The first observations pointing to this conclusion are those of Brown-Séquard. "There is always, even in mammals, after a transversal section of the whole or a lateral half of the spinal cord, at least some appearance of voluntary movements in the side of the injury, and always also a diminution of voluntary movements in the opposite side; so that, in animals, there seems to be in the spinal cord a decussation of a few of the voluntary motor conductors. As there seems to be no such decussation in man, at least according to several pathological facts, we shall not insist upon its existence in animals."[2]

Van Kempen has repeated and extended the very remarkable experiment of Galen, with the most satisfactory results. This observer made a median, longitudinal section of the cord in dogs and rabbits, at the site of the fifth, sixth, and seventh cervical vertebræ. "This experiment was followed by partial paralysis of voluntary movements in the posterior extremities, so that the animal thus operated upon moved the posterior limbs and was able to change his position, without, however, being able to raise himself."[3]

As there is some difference in the results of observations upon different animals, and as decussating motor fibres have never been demonstrated in man, it is impossible to apply the above experiments without reserve to the human subject; but they show, nevertheless, that, in mammals, the motor columns of the cord probably do not decussate in the

[1] GALENUS, *De Anatomicis Administrationibus*, Liber viii., Cap. vi.—*Opera omnia*, Lipsiæ, 1821, tomus ii., p. 683.

These remarkable experiments must have been made in the latter half of the second century, as Galen was born in 131, and died about the year 200.

[2] BROWN-SÉQUARD, *Physiology and Pathology of the Central Nervous System*, Philadelphia, 1860, p. 48.

[3] VAN KEMPEN, *Expériences physiologiques sur la transmission de la sensibilité et du mouvement dans la moelle épinère.—Journal de la physiologie*, Paris, 1859, tome ii., p. 528.

dorso-lumbar region; that partial decussation occurs in the cervical region; and that the decussation is completed in the anterior pyramids of the medulla oblongata.

Transmission of Sensory Impressions in the Cord.—There is very little room for discussion concerning what is positively known with regard to the transmission of sensory impressions in the cord, though there are some portions of its structure, the action of which in conduction is still obscure. Early in the physiological history of this portion of the nervous system, Longet made a number of experiments, which seemed to show that the posterior columns of the cord were the conductors of sensory impressions to the brain, and that the antero-lateral columns transmitted the motor stimulus. These have been already referred to in connection with the properties of the cord. They were made by applying a stimulus directly to the cord itself. Longet discredited observations made by dividing different portions of the cord, for the reason that he supposed that the mere operation of exposing the cord and of removing the dura mater was followed by a depression of the nervous action sufficient to render the evidences of sensibility in the lower extremities scarcely appreciable.[1] The conclusions drawn from these experiments were at first accepted by nearly all physiological writers, and it was generally admitted that the transmission of sensory impressions was effected solely by the posterior columns. It was found that the gray matter of the cord was both insensible and inexcitable, and the conduction was supposed to take place exclusively through the white substance. The views of Longet were in direct opposition to those of Bellingeri, who claimed, in 1823, to have demonstrated by experiment, that sensory impressions were conveyed to the brain exclusively by the gray substance of the cord, and that sensibility persisted in the lower ex-

[1] LONGET, *Anatomie et physiologie du système nerveux*, Paris, 1842, tome i., p. 276.

tremities after complete section of the posterior white columns.[1]

At the time the above-mentioned experiments were made, our knowledge of the properties of the cord was very incomplete, and it was difficult to understand how any of its fibres could conduct sensory impressions and yet be insensible to direct stimulation; but now we know that the gray matter does act as a conductor, and yet it is certainly insensible. The simple questions now to be determined are the following:

1. Does or does not the white substance of the posterior columns of the cord conduct sensory impressions to the brain?

2. Does the entire gray substance of the cord act as a conductor of sensation?

3. Do both the gray matter of the cord and the white substance of the posterior columns act as conductors, or does either one act to the exclusion of the other?

These questions may now be considered as definitively answered by the most positive and unmistakable results of experiments upon living animals, which, while they render the precise function of the white substance of the posterior columns a matter of conjecture, leave no doubt with regard to the parts of the cord which act as conductors of sensory impressions. This statement is based upon the researches of Brown-Séquard, whose experiments upon this subject have been often confirmed and never successfully contradicted.

The experimental answer to the first question is capable of but one construction. If the white substance of both posterior columns be divided, the sensibility of the posterior extremities is not diminished, at least as far as can be shown

[1] Bellingeri, *De Medulla Spinali Nervisque ex ea prodeuntibus, Annotationes Anatomico-Physiologicæ, Lectæ a die* 6 *januarii* 1822 *ad* 26 *januarii* 1823, p. 237; *Experimenta Physiologica in Medullem Spinalem habita, Lecta die* 13 *junii* 1824, p. 311; and Longet, *op. cit.*, tome iii., p. 341.

by experiments upon animals, in which these points are always difficult of determination. On the other hand, if every portion of the cord be divided except the posterior columns, sensibility is completely lost in the parts below the section. The accuracy of these results cannot be called in question, especially when controlled by experiments showing the conducting properties of the gray substance of the cord; and they show that, whatever may be the functions of the posterior white columns, they do not serve as conductors of sensory impressions.[1]

The second question admits of an equally positive answer from the results of experimental inquiry. If the entire substance of the cord, except the posterior columns of white matter, be divided transversely, as we have just seen, sensibility is abolished in all parts below the section; but, as we have stated in treating of the transmission of motor stimulus by the cord, voluntary motion is also destroyed.[2] Experiments show, farthermore, that sensory impressions are conveyed exclusively by the gray substance. "If the anterior, the lateral, and the posterior columns of the spinal cord

[1] The experiments by Brown-Séquard, which have led to the above conclusion, are of the most positive and satisfactory character (*Physiology and Pathology of the Central Nervous System*, Philadelphia, 1860, p. 19), and have been repeatedly confirmed by himself and other observers, among the most prominent of whom are Vulpian and Philipeaux (VULPIAN, *Système nerveux*, Paris, 1866, p. 373). The most important experiments in opposition are those of Schiff, quoted and adopted by Longet, by which Longet endeavors to prove that the posterior columns are conductors of the tactile sense (LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 353). In these experiments, the anterolateral columns were divided, and the animal was afterward enfeebled by a copious hæmorrhage. Upon pinching the tail, the animal gave evidence of sensation, but suffered no pain, even when the sciatic nerve was bruised or torn. In these observations, it was not shown that the entire gray substance was divided, and the experiments after copious hæmorrhage were certainly not made under strictly physiological conditions. It is well known, also, that if a small portion of gray matter be undivided, there is conduction of sensory impressions. In all of Brown-Séquard's experiments, the exact limits of the sections of the cord were ascertained by subsequent examination of the parts hardened in alcohol.

[2] See page 280.

are divided transversely, at the dorsal region, one set at one place, another at a distance of one or two inches, and the third also at the same distance from the second, so that the only channel of communication between the posterior limbs and the sensorium is the gray matter, of which, however, several parts have, unavoidably, been divided (such as the anterior and the posterior gray cornua, and also more or less of the central gray matter), we find that the posterior limbs are still sensitive, though evidently less than in the normal condition."[1]

It is impossible to divide the gray matter of the cord alone, without injuring, more or less, the white substance; but when the gray matter is divided with very slight injury of the white substance, sensibility in the parts below the point of section is totally destroyed.[2] As regards the part of the gray substance specially concerned in the transmission of sensory impressions, the results of experimental investigation have not been so definite; but Brown-Séquard is of the opinion that the transmission takes place chiefly in the gray matter surrounding the central canal, while it may also occur to some extent in other portions.[3]

The answer to the third question is deduced from the answers to the first two. The gray matter and the white substance of the cord do not participate in the transmission of sensory impressions, this being effected by the gray substance, especially its central portion, to the exclusion of the white.

The precise office of the posterior white columns of the cord is still a matter of conjecture. If these parts be insensible, except on the surface and near the posterior roots of the nerves, and if they take no part in the transmission of sensory impressions to the brain, which seems to have been conclusively proven, what is their function?

[1] Brown-Séquard, *Physiology and Pathology of the Central Nervous System*, Philadelphia, 1860, p. 22.

[2] Vulpian, *Système nerveux*, Paris, 1866, p. 374. [3] *Op. cit.*, p. 23.

The anatomical relations of the posterior white columns, the results of experiments upon living animals, and certain well-marked pathological phenomena, point very strongly to a connection between these columns and the coördination of muscular movements.

Probable Function of the Cord in Connection with Muscular Coördination.—Anatomists have not been able to trace satisfactorily the direction of all of the fibres contained in the posterior columns; but it is probable that at least some of these fibres serve as longitudinal commissures, and connect together the nerve-cells, extending for a greater or less distance both upward and downward in the cord. This anatomical arrangement is rendered probable chiefly by the results of experiments.

If the posterior columns be completely divided, by two or three sections made at intervals of from three-fourths of an inch to an inch and a quarter, the most prominent effect is a remarkable trouble in locomotion, consisting in a want of proper coördination of movements. These important experimental results were obtained by Vulpian.[1]

In the remarkable disease known under the name of locomotor ataxia,[2] there is a very peculiar condition of the muscular system, in which, while the power of the muscles is but slightly diminished, the movements of progression show great deficiency in coördinating power, frequently attended with more or less disturbance in the sensibility of the parts affected. These symptoms are associated with structural disease of the cord, limited to the posterior columns and the posterior roots of the spinal nerves.

Many years ago, before locomotor ataxia had been generally recognized by pathologists, Todd made the following remarkable statement with regard to the posterior columns:

[1] VULPIAN, *Système nerveux*, Paris, 1866, p. 381.

[2] For a description of this disease, see, HAMMOND, *Diseases of the Nervous System*, New York, 1871, p. 484, *et seq.*

"I have long been impressed with the opinion, that the office of the posterior columns of the spinal cord is very different from any yet assigned to them. They may be in part commissural between the several segments of the cord, serving to unite them and harmonize them in their various actions, and in part subservient to the function of the cerebellum in regulating and coördinating the movements necessary for perfect locomotion."[1] Todd further states, that this view is supported by the phenomena observed in cases of disease "distinguished by a diminution or total loss of the power of coördinating movements. . . . In two examples of this variety of paralysis, I ventured to predict disease of the posterior columns, the diagnosis being founded upon the views of their functions which I now advocate; and this was found to exist on post-mortem inspection; and in looking through the accounts of recorded cases in which the posterior columns were the seat of lesion, all seem to have commenced by evincing more or less disturbance of the locomotive powers, sensation being affected only when the morbid change of structure extended to and more or less involved the posterior roots of the spinal nerves."[2]

It is only necessary to add that the views of Todd have been in the main confirmed in the numerous cases of locomotor ataxia that have lately been so fully described by pathologists; and, from these facts, it is more than probable that the posterior columns contain fibres connecting the different segments of the cord, and that they play an important part in the coördination of muscular movements. The general function of coördination will be again considered in connection with the cerebellum.

Decussation of the Sensory Conductors of the Cord.—In hemiplegia due to injury of the brain, the paralysis occurs

[1] TODD, *Cyclopædia of Anatomy and Physiology*, London, 1839–1847, vol. iii., p. 721, Q, Article, *Nervous System.*

[2] *Op. cit.*, p. 721, R.

upon the side of the body opposite to the cerebral lesion. The phenomena ordinarily observed are simply paralysis of motion; but in those cases in which both motion and sensation are abolished upon one side of the body, the lesion in the brain is found to be upon the opposite side. It is evident, therefore, that there is a decussation of the conductors of sensory impressions as well as of the conductors of the motor stimulus.

As early as 1822, Fodéra made a longitudinal section of the spinal cord in the lumbar region, exactly in the median line. In this experiment, "sensation was destroyed, and in part motion upon the two sides."[1] Inasmuch as in this section it is only possible to divide the fibres passing from one lateral half of the cord to the other, it is evident that the sensory conductors must decussate in the spinal cord itself. As far as we know, this is the first experiment pointing to the decussation of sensory fibres in the cord, the observations of Galen, to which we have already referred, being limited to the phenomena of motion.[2]

The next experiments bearing upon the decussation of the sensory conductors in the cord are those of Van Deen. Among the numerous observations made upon the spinal cord by this physiologist, are one or two in which he noted the fact that, after section of one lateral half of the cord in the frog, at the site to the third dorsal vertebra, "the animal had no real loss of sensibility in the posterior extremity on the side on which the half of the spinal cord had been cut."[3] Although Van Deen did not distinctly state, as a conclusion drawn from these observations, that there is decussation of the sensory conductors in the cord, the fact of section of one lateral half of the cord with no loss of sensation on the cor-

[1] Fodéra, *Recherches expérimentales sur le système nerveux, présentées à l'Académie des sciences, le* 31 *décembre*, 1822.—*Journal de physiologie*, Paris, 1823, tome iii., p. 199.

[2] See page 284.

[3] Van Deen, *Traités et découvertes sur la physiologie de la möelle épinère*, Leide, 1841, pp. 65, 92.

responding side of the body remains as one of the first experimental arguments in favor of the crossed action.

Experiments upon living animals as well as pathological facts show that, after section or injury confined to one lateral half of the cord, the general sensibility upon the corresponding side of the body is very much exaggerated, producing a condition of well-marked hyperæsthesia. This remarkable fact was distinctly noted by Fodéra, in 1822: "Having divided, in a Guinea-pig, the right superior column of the cord in the middle of the dorsal region, the sensibility of the flank and of the posterior extremity of the same side was more exquisite than in every other part of the body, and it seemed that the movements of the same extremity possessed greater energy."[1] This observation was confirmed, and the experiments were very much extended, by Brown-Séquard.[2] Cases presenting the same phenomena have also been observed in the human subject, when one side of the cord has been invaded by disease.[3]

Physiologists are at a loss to explain the hyperæsthesia which follows section of the sensory conductors of the cord, but the fact nevertheless remains. The exaggeration of sensibility is not due to section of certain fibres, which might be supposed to increase the impressibility of the remaining fibres, for, as was shown by Vulpian, it is sufficient to prick with a pin one of the lateral halves of the cord to observe these remarkable phenomena.[4] With these few words, we will leave the subject of hyperæsthesia from injury to the cord, and pass to the crossed action of its sensory conductors.[5]

[1] Fodéra, *Journal de physiologie*, Paris, 1823, tome iii., p. 200.

[2] Brown-Séquard, *Experimental Researches applied to Physiology and Pathology*, New York, 1853, p. 64, *et al.*

[3] Brown-Séquard, *Recherches sur la transmission des impressions de tact, de chatouillement, de douleur, de temperature et de contraction (sens musculaire) dans la moelle épinère.—Journal de la physiologie*, Paris, 1863, tome vi., p. 645.

[4] Vulpian, *Système nerveux*, Paris, 1866, p. 388.

[5] For further experiments showing the effects of transverse section of the

In treating of the cord as a conductor of sensory impressions, we have already shown that this function is performed by the gray substance alone. We have also seen, in connection with the phenomena of conduction of the motor stimulus, that this is effected by the antero-lateral columns, which do not act as sensory conductors, except by virtue of their gray matter. As it is impossible to divide the gray matter with certainty without injuring the white substance, and as we are fully acquainted with the motor properties of the cord, we are prepared to comprehend the effects upon conduction of sensory impressions which follow division of one or the other lateral half. In our detail of experiments, we will not consider the phenomena of hyperæsthesia, but confine ourselves to the loss or diminution of sensibility.

Brown-Séquard was the first to demonstrate decussation of the sensory conductors in the cord itself; and, although his experiments upon this subject are almost innumerable, and his writings, scattered, voluminous, and sometimes not free from the obscurity due to unnecessary refinement and elaborateness of detail, the main facts can be expressed in a very few words; and he may justly be said to have created the physiology of the sensory conductors.

Brown-Séquard repeated the experiments of Galen and of Fodéra, dividing the cord longitudinally in the median line, producing complete paralysis of sensation on both sides in all the parts below the section. By this operation, if the section had been made accurately in the median line, the only fibres that could be divided were those passing from one side of the cord to the other.

The second experimental proof of the decussation of sensory fibres consists in transverse section of one or the other of the lateral halves of the cord. If one lateral half of the cord be divided, sensibility is abolished in the parts below

cord in its posterior portion, see, BROWN-SÉQUARD, *Nouvelles recherches sur la physiologie de la moelle épinère.—Journal de la physiologie*, Paris, 1858, tome i., p. 139.

the section upon the opposite side of the body. In an article published in 1858, Brown-Séquard details very succinctly an experiment showing this fact, though his first experiments were made in 1849.[1] He denuded the cord in the lumbar region in a vigorous dog, and made sections upon one side, progressively deeper and deeper, from without inward. When the section included about one-third of the lateral half, the sensibility seemed slightly augmented upon the opposite side. This section involved only a part of the lateral white column and a small portion of the anterior cornu of gray matter. When the section was extended so as to involve about two-thirds of the lateral half, the sensibility was notably diminished upon the opposite side. When the section extended to the median line, the sensibility was very much diminished; and when it extended just beyond the median line, it was entirely abolished upon the opposite side.[2] These observations, and others of the same nature, show conclusively that in the animals experimented upon, at least, there is a decussation of the greatest part of the sensory conductors in the cord itself.

The course of the fibres in their decussation is indicated by further experiments, which show that the sensitive fibres from the posterior roots of the nerves "pass along the posterior columns only a little way, and leave them to enter the central gray matter."[3] It is undoubtedly in this gray substance that they pass from one side to the other, probably through the cell-prolongations. The fact that the fibres pass in the cord a short distance before they decussate, and that they pass downward as well as upward, is well shown by the following experiment:

"If we divide transversely a lateral half of the spinal

[1] See list of works, in the *Journal de la physiologie*, Paris, 1862, tome v., p. 646, No. 44.

[2] BROWN-SÉQUARD, *Nouvelles recherches sur la physiologie de la moelle épinère.—Journal de la physiologie*, Paris, 1858, tome i., p. 139, *et seq.*

[3] BROWN-SÉQUARD, *Physiology and Pathology of the Central Nervous System.* Philadelphia, 1860, p. 25.

cord in two places, so as to have three pairs of nerves between the two sections, we find that the middle pair has almost the same degree of sensibility as if nothing had been done to the spinal cord, while the two other pairs have a diminished sensibility, the upper one particularly in its upper roots, and the lower one in its lower roots; which facts seem to show that the ascending fibres of the upper pair, and the descending fibres of the lower one, have been divided before they had made their decussation.

If there is only one pair of nerves between two sections, its sensibility is almost entirely lost, as then the transversal fibres are almost alone uninjured (most of the ascending and descending being divided), which fibres are employed for reflex action, and hardly for the transmission of sensitive impressions."[1]

The experimental facts just cited conclusively show decussation of sensory conductors in the cord in the animals operated upon, and this has been sufficiently confirmed by other experimenters to render the fact certain. It is possible that the decussation may not be so complete in some other classes of animals, which would account for the results obtained by those who have denied decussation; but cases of disease of the cord in the human subject all go to show that the crossed action is complete in man.

Summary of the Action of the Spinal Cord as a Conductor.

The antero-lateral columns of the cord, comprising that portion included between the anterior median fissure and the origin of the posterior roots of the nerves, are insensible to direct irritation, and serve as conductors of the motor stimulus from the brain to the anterior roots of the nerves. If these columns be divided, voluntary motion is lost in all parts below the section. If the rest of the cord be divided, leaving the antero-lateral columns intact, the power of volun-

[1] BROWN-SÉQUARD, *Central Nervous System*, Philadelphia, 1860, p. 36.

tary motion remains. Throughout the greater part of the cord, this action is direct, and division of the antero-lateral columns on one side produces paralysis of motion on the corresponding side of the body. There is a decussation of the motor fibres at the medulla oblongata, and a partial decussation in the cord itself in the upper cervical region. In the dorsal region and below, the motor conducting fibres are situated chiefly in the anterior columns; but in the cervical region, these fibres pass to the sides and are contained chiefly in the lateral columns. The conduction of motor stimulus is probably not effected exclusively by the white substance, but is transmitted in part by the gray matter.

The gray substance of the cord serves as the medium of transmission of sensory impressions to the brain. This is effected chiefly by the gray matter surrounding the central canal, but it may take place to some extent in other portions. If the entire gray matter be divided, with but slight injury to the white substance, sensation is lost in all parts situated below the section. The white substance does not conduct sensory impressions to the brain, either in the antero-lateral or the posterior columns. The most probable function of the white substance of the posterior columns is to unite the different segments of the cord together by longitudinal commissural fibres; and this portion of the cord has an important influence in coördinating the muscular movements.

The sensitive nerve-fibres from the posterior roots of the spinal nerves pass in the cord for a short distance upward and downward. They then penetrate the gray matter, and decussate throughout the entire length of the cord. Division of one lateral half of the cord is followed by complete paralysis of motion on the corresponding side of the body in all parts below the section; anæsthesia in all parts below the section, on the opposite side of the body; and hyperæsthesia in the parts below the section, upon the corresponding side of the body.

The anatomical points bearing upon the physiological action of the cord are the following:

The fibres from the anterior roots penetrate the anterior gray cornua directly and are in immediate connection with the prolongations of the motor cells. The motor cells also have prolongations which pass to the brain in the white substance. The motor fibres are thus directly connected with the cellular elements of the cord, the elements probably concerned in reflex movements, and the cells are in connection with conducting fibres to the brain.

The fibres from the posterior roots take several directions. Some of them pass to the gray substance. A portion passes to the posterior columns, some extending upward and others downward. The decussation, which is rendered certain by physiological experiments, has not been satisfactorily followed by anatomists. It undoubtedly takes place in the gray substance, probably in part by a crossing of the fibres themselves, and in part by a crossing of prolongations from the cells with which certain fibres from the posterior roots are connected.

CHAPTER XI.

ACTION OF THE SPINAL CORD AS A NERVE-CENTRE.

Movements in decapitated animals—Definition and applications of the term "reflex"—Reflex action of the spinal cord—History of the discovery of so-called reflex action—Question of sensation and volition in frogs after decapitation—Character of movements following irritation of the surface in decapitated animals—Dispersion of impressions in the cord—Conditions essential to the manifestation of reflex phenomena—Exaggeration of reflex excitability by decapitation, poisoning with strychnine, etc.—Reflex phenomena observed in the human subject.

It has long been known that decapitation of animals does not immediately arrest muscular action; and the movements observed after this mutilation present a certain degree of regularity, and, of late years, have been shown to be in accordance with well-defined laws. Under these conditions, the regulation of such movements is effected through the spinal cord and the nerves connected with it. If an animal be decapitated, leaving only the cord and its nerves, there is no sensation, for the parts capable of appreciating sensation are absent; nor are there any true voluntary movements, as the organ of the will is destroyed. Still, in decapitated animals, the sensory nerves are for a time capable of conducting impressions, and the motor nerves can transmit a stimulus to the muscles; but the only part capable of receiving an impression or of generating a motor stimulus is the gray matter of the cord. If, in addition to the removal of all of the encephalic ganglia, the cord itself be destroyed, all movements of voluntary muscles are abolished, except as they may be

produced by direct stimulation of the muscular tissue or of individual motor nerves.

We must regard the gray matter of the brain and spinal cord as a connected chain of ganglia, capable of receiving impressions through the sensory nerves, and of generating the so-called nerve-force. The great cerebro-spinal axis, taken as a whole, has this general function; but some parts have separate and distinct properties, and can act independently of the others. The cord, regarded as a conductor, connects the brain with the parts to which the spinal nerves are distributed. If the cord be separated from the brain in a living animal, it may act as a centre, independently of the brain; but the encephalon has no communication with the parts supplied with nerves from the cord, and can only act upon the parts which receive nerves from the brain itself.

It has been pretty clearly shown that when the cord is separated from the encephalon, an impression made upon the general sensory nerves is conveyed to its gray substance, and is transformed, as it were, into a stimulus, which is transmitted to the voluntary muscles, giving rise to certain movements, independently of sensation and volition. This impression is said to be reflected back from the cord through the motor nerves; and the movements occurring under these conditions are called reflex. As they are movements excited by stimulation of sensory nerves, they are sometimes called excito-motor.

The term reflex may properly be applied to any generation of nerve-force which occurs as a consequence of an impression received by a nerve-centre; and reflex phenomena are by no means confined to the action of the spinal cord. The movements of the iris are reflex, and yet they take place in many instances without the intervention of the cord. The movements of respiration are reflex, and these are presided over by the medulla oblongata. Movements of the intestines and the involuntary muscles generally are reflex, and they involve the action of the sympathetic system of

nerves. Impressions made upon the nerves of special sense, as those of smell, sight, hearing, etc., give rise to certain trains of thought. These involve the action of the brain; still they are reflex. In this last example of reflex action, it is sometimes difficult to connect the operations of the mind with external impressions as an exciting cause; but it is evident, from a little reflection, that this is often the case. This fact is illustrated by operations of the brain which take place, as it were, without consciousness, as in dreams. It has been clearly shown that a particular direction may be given to the thoughts during sleep, by impressions made upon the sense of hearing. A person sleeping may be made to dream of certain things, as a consequence of hearing peculiar noises. Examples of this kind of mental reflex action are sufficiently numerous and well authenticated.[1]

From the above considerations, it is evident that the term reflex may be properly used in connection with many phenomena involving the action of the sympathetic system and of the brain; but it is generally understood as applying especially to involuntary movements, occurring without consciousness, as the result of impressions made upon the afferent nerves, and involving the independent action of the spinal cord.

Reflex Action of the Spinal Cord.—In 1832 and 1833, Marshall Hall described minutely the movements which take place in decapitated animals as a consequence of stimulation of the sensory nerves, and formularized these phenomena under the head of "the reflex function of the medulla oblongata and medulla spinalis."[2] Since this publication, a new interest has been attached to the writings of some of the older physiologists, in which reflex action, as it is now

[1] For numerous instances of peculiar dreams referable to external impressions received during sleep, see, HAMMOND, *Sleep and its Derangements*, Philadelphia, 1869, p. 127, *et seq.*

[2] MARSHALL HALL, *On the Reflex Function of the Medulla Oblongata and Medulla Spinalis*, London, 1833.

understood, had been mentioned more or less definitely. In the history of important advances in physiological knowledge, it has often been the case that discoveries have been foreshadowed by the earlier writers; and bibliographical research shows that the literature of the cord as a nerve-centre forms no exception to this, which is almost the rule. Some of the allusions to the cord as a centre of reflex action, made anterior to 1833, are vague and indefinite; but, on the other hand, certain excito-motor actions were very accurately described, as early as 1812. Marshall Hall grouped and classified these phenomena, and showed their relations to the cord as an independent centre; but, as we shall see, he has no claim to the title of the discoverer of reflex action, and his experiments presented little that was really new.

Whytt, in his work on the "Vital and other Involuntary Motions," states that the involuntary and mixed motions proceed from a stimulus, the latter being partly, and the former not at all, under the power of the will;[1] and, by a stimulus, he means an impression made upon the sensory nerves.

Prochaska, who wrote between 1778 and 1797, states that the sensorium commune extends to the medulla spinalis, and that this "is manifest from the motions exhibited by decapitated animals, which cannot take place without the consentience and intervention of the nerves arising from the medulla spinalis; for the decapitated frog, if pricked, not only withdraws the punctured part, but also creeps and leaps, which cannot be done without the consensus of the sensorial and motor nerves, the seat of which consensus must necessarily be in the medulla spinalis—the remaining portion of the sensorium commune."[2] He calls this "reflexion," and speaks of it as taking place without consciousness, describing many phenomena now familiarly known as reflex.

[1] Whytt, *Works*, Edinburgh, 1768, p. 170.

[2] Prochaska, *A Dissertation on the Functions of the Nervous System*, Sydenham Society, London, 1851, p. 430.

Legallois published, in 1812, a remarkable memoir on the principle of life. In this work, he details numerous experiments, many of them on the nervous system, and of great interest in connection with the present question. In the rabbit, after division of the cord in the lumbar region, Legallois showed that "sensation and voluntary motion continued to take place, even in the posterior extremities. But there is no longer any connection in sensation or movement between the anterior parts and the parts posterior to the section of the cord; that is to say that, if the tail or, indeed, one of the hind-feet be pinched, the entire posterior parts are agitated, but the anterior parts seem to feel nothing, and do not move."[1]

Passing over a few confirmatory observations by other experimenters, we come to those of Fodéra, in 1822. Fodéra states that "in wounds of the spinal cord, the animal suffers pain and convulsions; if it be divided transversely, there is paralysis of the posterior parts, with loss of sensation and motion. But irritation applied below the section produces agitation of the muscles to which the nerves derived from it are distributed. The animal does not suffer pain, for it has no consciousness of what takes place in these parts."[2] Again, Fodéra says: "With regard to the spinal cord, complete transverse section in birds does not in general entirely paralyze the posterior extremities; if we pinch the foot, they withdraw it, although they suffer no pain from it; but if the spinal cord be entirely destroyed in the interior of the vertebral canal, the paralysis is perfect."[3] At about the same time, Mayo described, even more definitely than his predecessors, the reflex function of the cord, in the following words:

[1] LEGALLOIS, *Expériences sur le principe de la vie.—Œuvres*, Paris, 1824, p. 80.

[2] FODÉRA, *Recherches expérimentales sur le système nerveux, Présentées à l'Académie des sciences le* 31 *décembre*, 1822.—*Journal de la physiologie*, Paris, 1823, tome iii., p. 196.

[3] *Op. cit.*, p. 214.

"On the one hand, it is clear that an influence, independent of the will, occasionally throws voluntary muscles into action, as appears in tetanus and other spasmodic disorders; and is shown remarkably in the physiological experiment of irritating the skin on the lower extremities, after the division of the spinal cord in the back, when the occurrence of action limited to the muscles of the inferior extremities, evinces that a connection exists, independently of the will, between sentient surfaces and the action of voluntary muscles. I have varied this experiment by dividing the spinal cord at once in the neck and in the back, upon which three unconnected nervous centres exist; and the division of the skin of either part (and especially at the soles of the feet, in the two hinder portions) produces a convulsive action of the muscles of that part alone. The same influence may, then, possibly regulate the unconscious actions to which these remarks relate."[1]

The experiments of Marshall Hall, published in 1832 and 1833, are familiar to every physiologist, as supplying nearly all of the omissions of the observers just cited. The points which he assumed to have experimentally demonstrated by his researches are as follows: A decapitated animal, the only part of the cerebro-spinal axis which remains being the spinal cord, will make no movements, if completely protected from all external impressions. An impression made upon the sensory nerves of a decapitated animal is reflected by the cord, through the motor nerves, to the muscles, and gives rise to reflex movements. If the cord be destroyed, no movements follow stimulation of the surface. If the centripetal and the centrifugal nerves be divided, no reflex movements can take place. Experiments upon decapitated animals accord with the results of observations upon acephalous fœtuses, and in cases of complete paraplegia from injury to the cord. All of the involuntary movements

[1] Mayo, *Anatomical and Physiological Commentaries*, Number II., July, 1823, London, 1823, p. 17.

observed in the healthy body are explained by the theory of reflex action.[1] These observations of Marshall Hall were, in the main, confirmed by Müller, the year succeeding their first publication;[2] and, by some writers, the credit of the discovery of the mechanism of reflex action is given to both Müller and Marshall Hall.

From the point of view which the present condition of science enables us to take with regard to the reflex action of the cord, we have to determine the accuracy of the observations of Marshall Hall, and to follow out the advances that have been made by more recent observers. It is important, as the first step in our inquiry, to ascertain the exact condition of decapitated animals as regards their capacity for muscular movements; and upon this point there is some difference of opinion. Marshall Hall thought that an animal, a frog, for example, after decapitation, was incapable of any voluntary movement, or of any movement which did not have, for its exciting cause, an external impression. We take the example of frogs, because these are the animals most commonly used by experimenters.

All who have experimented upon frogs have seen them jump about vigorously after decapitation; and the question whether these be spontaneous movements, so called, or an excito-motor action, is more difficult to determine than would at first sight appear. It would be unphilosophic to assume that because the animal has been decapitated, the movements are due to external impressions only, if we use this as evidence against the possibility of spontaneous movements under these conditions. The obvious necessity of the argument is to remove all possibility of external impressions, or of irritation of the cord itself. Upon this

[1] MARSHALL HALL, *Reflex Function of the Medulla Oblongata and Medulla Spinalis*, London, 1833; and, *Memoirs on the Nervous System*, London, 1837. Marshall Hall states that his first publication appeared in the Proceedings of the Zoological Society, in 1812.

[2] MÜLLER, *Elements of Physiology*, translated by Baly, London, 1840, pp. 761, 799.* The first edition of Müller's work was published in Berlin, in 1833.

point we can only speak positively from our own experiments. If a frog be decapitated, so as to leave only the spinal cord intact, if we wait for from one to three minutes until the effects of the shock and local irritation have subsided, if we then, when the animal has become perfectly quiet, cover it with a bell-glass, and finally, if we remove all possibility of jarring the table on which the animal is placed, there is no movement of muscles. In making an experiment of this kind, we occasionally see movements which are due to a very feeble impression, such as a breath of air, or a jar from the street, but which is perfectly evident to the observer; and, when a movement is once made, this gives rise to another impression, and thus, successive actions of the muscles may take place. The movements in jumping are so simple that they seem, sometimes, under these conditions, to be voluntary. The effect of feeble excitations is also very marked in animals poisoned with strychnine; but, even here, we do not have movements, unless an impression be first made upon the sensory nerves. When we come to experiments upon the mammalia, there can hardly be any question of this kind; for here, as the rule, no movements are observed after the encephalic ganglia have been removed, unless the sensory nerves be pretty strongly stimulated. Analogous phenomena are observed in the lower extremities, in cases of paraplegia in the human subject.

The next important question to determine is with regard to the nature of movements excited by external stimulation in decapitated animals, especially frogs; for some of these movements are so regular as to appear to be connected with sensation and volition. The experiments of Pflüger upon this point are very remarkable. These have been repeatedly confirmed, and there can be no doubt with regard to their accuracy. Pflüger carefully removed from a frog the entire encephalon, leaving only the spinal cord. He then touched the surface of the thigh over the inner condyle with acetic acid, to the irritation of which frogs are peculiarly sensitive.

The animal thereupon rubbed the irritated surface with the foot of the same side, apparently appreciating the locality of the irritation, and endeavoring, by a voluntary effort, to remove it. The foot of this side was then amputated, and the irritation was renewed in the same place. The animal made an ineffectual effort to reach the spot with the amputated member, and, failing in this, after some general movements of the limbs, rubbed the spot with the foot of the opposite side.[1] Although this experiment does not always progress precisely in the manner described, it has succeeded perfectly in so many instances as to lead some physiologists to conclude that sensation and volition are not entirely abolished by removal of the encephalon, at least in frogs.[2]

The remarkable phenomena just detailed are to be regarded from two points of view: first, with reference to their bearing upon the question of the existence of perception and volition in the spinal cord of the frog; and second, the question of the application of these phenomena to the physiology of the cord in man and the higher classes of animals. The conditions of the experiment in the frog are simply these: Instead of exposing the surface to a single and instantaneous stimulation, the excito-motor effects of which are observed as a direct response to the irritation, and immediately cease, we have, by the application of acetic acid to the surface, a prolonged impression upon the sensory nerves, which, by virtue of the anatomical connections between the different parts of the cord, is probably dispersed throughout the entire spinal axis. That powerful impres-

[1] Pflüger, *Die sensorischen Functionen des Rückenmarks der Wirbelthiere*, Berlin, 1853, S. 124, *et seq.*

[2] Observations of very much the same character as those of Pflüger were published by Paton, in 1858. He refers to experiments showing the perceptive power of the cord, by Dr. Dowler, of New Orleans, but does not allude to the experiments of Pflüger. (Paton, *On the Perceptive Power of the Spinal Cord as manifested by Experiments on Cold-blooded Animals.—North American Medico-Chirurgical Review*, Philadelphia, 1858, vol. ii., pp. 467, 703). These observations have been repeatedly confirmed by other physiologists.

sions may be thus dispersed, there can be no doubt, as we shall see farther on. The phenomena under consideration certainly point to an appreciation by the cord of the locality of a powerful impression, and this could be manifested in an animal only by an apparent muscular effort to reach the irritated spot; but we can hardly reason from this fact, that in man and the higher animals, the spinal cord shares with the brain the power of appreciating what we know as sensation and of generating the stimulus of true voluntary movement. If a sudden and very powerful painful impression be made upon the surface in man under normal conditions, the hand may be instantly applied to the affected part, apparently before we really appreciate the pain or have time to make a distinct effort of the will; but the connections between the different parts of the cerebro-spinal axis do not permit us to isolate the action of the cord. Certain it is that, in the higher animals, after removal of the encephalon, and in experiments upon decapitated criminals and patients suffering from paraplegia, there is no evidence of true sensation or volition in the spinal cord; and in man and the higher animals, we must regard all muscular movements which depend solely upon the action of the cord as a nerve-centre as automatic and entirely independent of consciousness and of the will.

It is easy to determine, by experiments to which we have already incidentally alluded, that the muscular movements dependent upon nervous action, occurring in decapitated animals, are due to the action of the spinal cord as a nerve-centre. In an animal in which the reflex phenomena are very marked, as they are after decapitation, especially if the animal be poisoned with strychnine or opium, all movements cease immediately when the cord is destroyed. That the gray matter of the cord is the part concerned as a centre in the production of these phenomena, is probable, in view of what we know with regard to the general functions and properties of this substance; and experiments have shown that this is the fact. If, in a decapitated frog, we make a

longitudinal section of the cord in the median line, leaving only a slight communication between the two sides, we may sometimes succeed, by strongly irritating the skin of one leg, in producing reflex movements, not only in the same leg, but in the leg of the opposite side; and it is reasonable to suppose that the irritation is propagated from one side to the other through the cells of the gray matter.[1]

The conditions essential to the manifestations of reflex phenomena depending upon the action of the cord are very simple and easily understood.

In the first place, it is necessary that one or more of the posterior roots of the spinal nerves should be in communication with the cord, in order to conduct the impression to this nerve-centre. If all of the posterior roots be divided, there is no nervous communication between the periphery and the centre, and no movements follow irritation of the surface. When the excitability of the cord is exaggerated, as in poisoning by strychnine, a single posterior root is sufficient to conduct an impression to the cord, which will give rise to violent contractions of all the muscles.[2] This is due to a dispersion of the impression, under these conditions of increased excitability, from the single point of entrance of the posterior root, throughout the cord. In animals that have been simply decapitated, a similar dispersion of impressions may also take place. If a comparatively feeble single impression be made upon any part of the general surface, as the rule, the subjacent muscles only are the seat of contraction; but if the impression be more powerful, or if it be prolonged, as when we apply a drop of acetic acid to any part of the skin of a frog, this impression may be diffused throughout the cord, producing contractions of the general muscular system. We have already shown, in treating of the general properties of the sensory nerves, that an impression made at any point in the course of a nerve is conducted to the centre. Reflex

[1] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 260.

[2] BERNARD, *Système nerveux*, Paris, 1858, tome i., p. 342.

movements may, consequently, be produced by stimulating the sensory nerves in their course, or by irritating the posterior roots of the spinal nerves.

We have already stated that the cord must retain its anatomical integrity, in order to receive an impression made upon the centripetal nerves, and transform it, as it were, into a stimulus, which is reflected back by the motor nerves and produces muscular contraction. It is also evident that the motor nerves must retain their connection with the cord, and be in a condition to conduct the stimulus reflected by the cord to the muscles.

The reflex excitability of the spinal cord is increased to a marked degree by separating this portion of the cerebro-spinal axis from the encephalon, and the same is true for the lower portion of the cord, when a section is made in the dorsal or the lumbar region. It is difficult to find an entirely satisfactory explanation of this fact; and the phenomena observed under these conditions are, in this regard, like the exaggerated sensibility of portions of the general surface after section of certain columns of the cord. Setschenow proposed, some years ago, the theory that the reflex excitability of the cord under natural conditions was subject to a moderating, or an inhibitory influence from the encephalon; and that this influence being absent in decapitated animals, the excitability of the cord, under these conditions, seemed to be exaggerated.[1] Whether this explanation be accepted or not, the fact remains, that reflex phenomena are more easily excited and are more marked in animals after decapitation, than in the same animals, when the connections between the cord and brain have not been destroyed. In addition, Vulpian has shown that the excitability is intense in proportion as the part of the cord con-

[1] SETSCHENOW, *Physiologische Studien über die Hemmungsmechanismen für die Reflexthätigkeit des Rückenmarks im Gehirne des Frosches*, Berlin, 1863; and, SETSCHENOW UND PASCHUTIN, *Neue Versuche am Hirn und Rückenmark*, Berlin, 1865.

cerned in the reflex phenomena is restricted; and, after section of the cord itself, the most powerful and easily-excited movements are produced when the division has been made low down in the lumbar region. He has also shown that simple puncture of the cord produces an exaggeration of the reflex excitability, as well as hyperæsthesia.[1]

In experiments upon animals, the reflex phenomena are greatly exaggerated in intensity in the tetanic condition produced by poisoning by opium or strychnine. Take, for example, a frog decapitated and poisoned with strychnine. No reflex movements occur unless an impression be made upon the sensory nerves; but the faintest irritation, such as a breath of air or a slight jar, throws the entire muscular system into a condition of violent tetanic spasm. The same phenomena are observed in cases of poisoning by strychnine, or of tetanus, in the human subject. This fact is important in its relations to the treatment of these conditions; for it is evident that, in such cases, the exhaustion due to the violent spasms may be moderated by carefully avoiding all unnecessary irritation of the surface.

It was shown a number of years ago, by Longet, that the inhalation of anæsthetic agents may abolish all of the ordinary reflex phenomena.[2] Whether this be due to an action upon the cord itself or to a paralysis of the sensory nerves, it is difficult to determine. Ordinarily, in animals rendered insensible by anæsthetics, the reflex act of respiration continues; but this may also be arrested, as has been observed by all who have experimented with anæsthetics, especially with chloroform. A common way of determining that an animal is completely under the influence of ether is by an absence of the reflex act of closing the eyelids when the cornea is touched.

It now only remains to show that the phenomena of reflex action observed in experiments upon the inferior ani-

[1] Vulpian, *Système nerveux*, Paris, 1866, pp. 441, 442.

[2] Longet, *Traité de physiologie*, Paris, 1869, tome iii., p. 256.

mals, especially frogs, are applicable to the human subject, and to indicate the muscular actions which depend upon the cord as a nerve-centre.

It is only necessary, after what has gone before, to indicate in a general way the phenomena observed in the human subject which illustrate the reflex action of the cord. It is a common observation, in cases of paraplegia in which the lower portion of the cord is intact, that movements of the limbs follow titillation of the soles of the feet, these movements taking place independently of the consciousness or the will of the subject experimented upon. Acephalous fœtuses will present reflex movements, movements of respiration, and will even suck when the finger is introduced into the mouth. Observations of this kind are so numerous and familiar, that they need not be cited in detail. Experiments have also been made upon criminals after decapitation; and although the reflex phenomena are not so well marked and cannot be excited so long after death as in cold-blooded animals, they are sufficiently distinct. In 1869, quite an elaborate series of investigations of this kind was made by Robin.[1]

It is difficult, in studying, in the human subject, the ordinary phenomena of movements in the voluntary muscular system, to isolate the reflex phenomena from those acts involving sensation and volition. In many persons, titillation of the soles of the feet produces violent contractions of muscles, which cannot be arrested by an effort of the will, and this may even be followed by general convulsions. When we unexpectedly touch an irritating surface with the hand, the muscles of the arm act so quickly, that we may suppose that this takes place before we really appreciate the painful sensation; and, if the impression be very severe, we may have movements more or less general. Operating upon highly-sensitive parts, it is frequently impossible to arrest re-

[1] Robin, *Observations anatomiques et physiologiques faites sur des suppliciés par décollation.—Journal de l'anatomie*, Paris, 1869, tome vi., p. 69, *et seq.*

flex movements, as the closing of the eyelids when the cor nea is touched. True reflex movements may be produced by carefully-executed experiments upon persons asleep. We cannot arrest the act of vomiting induced by titillation of the fauces; and other instances of this kind might be cited.

Most of the true involuntary movements are reflex; but these have been or will be considered under their proper heads. The movements of deglutition depend upon an impression made upon the mucous membrane of the pharynx, etc. The movements of respiration are excited by an impression made upon the general sensory nerves, due to want of oxygen, as we have shown in treating of respiration. The ejaculation of semen is also reflex. Important reflex actions take place through the sympathetic nerves, such as the movements of the intestines, vaso-motor movements, etc.; but these will be considered fully under the head of the sympathetic system. Secretion, the action of the heart, the contractions of the uterus, the action of the sphincters, the movements of the iris, etc., take place through the sympathetic and the cerebro-spinal system.

As regards the farther action of the cord as a nerve-centre, there are undoubtedly many functions influenced more or less by this portion of the cerebro-spinal axis; but these have been treated of under their appropriate heads, or will be considered hereafter.

CHAPTER XII.

THE CEREBRAL HEMISPHERES.

Physiological divisions of the encephalon—Weight of different parts of the brain and of the entire encephalon—Some points in the physiological anatomy of the encephalon and its connections—The cerebrum—General properties of the cerebrum—Functions of the cerebrum—Extirpation of the cerebrum in animals—Pathological facts bearing upon the functions of the cerebrum—Comparative development of the cerebrum in the lower animals—Development of the cerebrum in different races of men and in different individuals—Ethnological table, derived from autopsies of white and negro brains—Table of weights of the encephalon in different individuals—Location of the faculty of articulate language in a restricted portion of the anterior cerebral lobes.

The anatomy of the encephalon is so complex, that it can be treated of with advantage only by a very minute and carefully-illustrated description, such as is to be found in some of the elaborate anatomical works or in special treatises on the nervous system. We shall not consider under a distinct head the general physiological anatomy of the brain, for the reason just given, and also because we are as yet ignorant of the exact connection between the structure and arrangement of many of its parts and their physiology. We know that the gray substance is capable of appreciating general and special impressions received by the peripheral nervous system, and of generating the so-called nerve-force. Impressions are conveyed to this portion of the cerebro-spinal axis by the sensory conductors, passing to the brain, either through the cord or by the cranial nerves, and by the nerves of special sense, as well as those of general sensibility. The stimulus

which gives rise to voluntary movements is generated in the brain, and is conveyed by the motor nerves to the appropriate muscles. We have seen, also, that the centres of the encephalon may be concerned in reflex action. In addition, parts of the brain act as centres of sensation and volition and are concerned in the varied phenomena of intellection.

The encephalon, or what is ordinarily known as the brain, consists of a number of ganglia, or collections of gray matter, connected with each other, and also, by the different columns of the cord, with the motor and sensory nerves of the general system. Certain of these ganglia have separate and distinct functions, which are more or less completely understood; while there are, in addition, masses of gray substance, the physiological relations of which are as yet obscure or entirely unknown. The greatest and the most important of all, the gray matter of the cerebral hemispheres, undoubtedly has subdivisions connected with distinct attributes of the mind; but our positive knowledge with regard to these divisions is, at the present day, very meagre, though this subject has long been a favorite field for philosophic speculation.

Confining ourselves strictly to the limits of positive information, we may recognize the following parts of the encephalon as distinct ganglia: 1. The gray matter of the cerebral hemispheres; 2. The gray matter of the cerebellum; 3. The olfactory ganglia; 4. The gray matter of the corpora striata; 5. The gray matter of the optic thalami; 6. The tubercula quadrigemina; 7. The gray matter of the tuber annulare, or pons Varolii; 8. The ganglion of the medulla oblongata. In addition, the following parts have been made the subject of physiological investigation or speculation, with results more or less definite. The peduncles of the cerebrum and of the cerebellum; the pineal gland; the corpus callosum; the septum lucidum; the cerebral ventricles; and the pituitary body. We have, however, little if any positive information concerning these parts, except their general anatomical relations; and their physiology really amounts to little more than a

history of the vague speculations of the ancients or the fruitless experiments of modern observers. It is to be hoped that future anatomical investigations, chiefly in following out the course of the fibres of the encephalon and their connections with the cells of the different collections of gray matter, will throw light upon the functions of this part of the cerebro-spinal axis; but at present, all physiologists will admit that we have received very little aid from this source. In our anatomical descriptions, therefore, we shall confine ourselves to those points that are strictly physiological.

Weight of different Parts of the Brain and of the entire Encephalon.—Most of the tables of the weight of the healthy adult brain of the Caucasian, given by different observers, show essentially the same results, the differences amounting to only one or two ounces for the entire encephalon. The average given by Quain is 49½ ounces, avoirdupois, for the male, and 44 ounces for the female. This is the general result obtained by combining the tables published by Sims, Clendinning, Tiedemann, and Reid. The number of male brains weighed was 278, and of female brains, 191. In males, the minimum weight was 34 ounces, and the maximum, 65 ounces. In 170 cases out of the 278, the weight ranged from 46 to 53 ounces, which may be taken as the general average. In females, the minimum was 31 ounces, and the maximum, 56 ounces. In 125 cases out of the 191, the weight ranged from 41 to 47 ounces.

Quain assumes, from various researches, that in newborn infants, the brain weighs 11·65 ounces, for the male, and 10 ounces, for the female. In both sexes, "the weight of the brain generally increases rapidly up to the seventh year, then more slowly to between sixteen and twenty, and again more slowly to between thirty-one and forty, at which time it reaches its maximum point. Beyond that period, there appears a slow, but progressive diminution in weight

of about one ounce during each subsequent decennial period; thus confirming the opinion, that the brain diminishes in advanced life."

The comparative weights of the several parts of the encephalon, calculated from observations on the brains of fifty-three males and thirty-four females, between the ages of twenty-five and fifty-five, are as follows:

	Males.	Females.
Average weight of cerebrum	43·98 oz.	38·75 oz.
Average weight of cerebellum	5·25 "	4·76 "
Average weight of pons and medulla oblongata.....	0·98 "	1·01 "
Average weight of entire encephalon......	50·21 oz.	44·52 oz.

The proportionate weight of the cerebellum to that of the cerebrum, in the male, is as 1 to $8\frac{4}{7}$, and in the female, as 1 to $8\frac{1}{4}$.

The specific gravity of the whole encephalon is about 1,036, that of the gray matter being 1,034, and of the white, 1,040.[1]

The above weights are quoted from Quain's admirable work on anatomy, and the normal range of variations and averages only are given. When we come to treat of the cerebrum and its relations to intelligence, we will discuss the weights of the brain in idiots and in persons of extraordinary intellectual power, as far as any data upon these points are to be found.

Some Points in the Physiological Anatomy of the Encephalon and its Connections.—The direction of the fibres in the encephalon, their connections with the cells of the gray substance, the course of commissural fibres connecting together the different parts of the gray substance of the cerebrum, the cerebellum, and the deeper ganglia, and finally the avenues of communication between the fibres of the encephalon and the cord, are points of exceeding intricacy;

[1] QUAIN, *Elements of Anatomy*, London, 1867, vol. ii., p. 568, *et seq.*

and many of them are still so uncertain and obscure, that they cannot as yet be connected satisfactorily with the exact results of physiological inquiry. All that we can do at present, is to recognize certain ganglionic masses, the separate functions of which have been more or less accurately defined, and show, as far as possible, their anatomical relations to each other and to the cord.

The separate collections of gray matter concerning which we possess positive physiological knowledge are, the gray matter of the cerebral hemispheres and of the cerebellum, the corpora striata, optic thalami, tuber annulare, or pons, and the medulla oblongata. To these may be added, the olfactory ganglia, which preside over the sense of smell, and the tubercula quadrigemina, or optic lobes, which are the centres connected with vision. The minute anatomy of the nerve-fibres and the nerve-cells, with their mode of connection with each other, have been already considered with sufficient minuteness under the head of the general structure of the nervous system.[1] We shall here discuss chiefly the direction of the fibres through which the encephalic ganglia are connected with the periphery, the fibres connecting the different ganglia with each other, and, in the case of the larger ganglia, certain commissural fibres connecting together their different parts.

In the wealth of literature pertaining to the minute anatomy of the encephalon, it is somewhat difficult to separate and define the well-established facts which have a direct bearing upon physiology. Perhaps the most elaborate and, to a certain extent, the most satisfactory observations upon the various points to be considered, are those of Luys; but this author describes the course of the fibres with an exactitude that seems hardly justified, in all instances, by the facts, in view of the inevitable difficulty and uncertainty of some of the processes employed; and the graphic and admirable delineations by which the work is illustrated, though profess-

[1] See Chapter I.

edly schematic, present a degree of ideality which inspires some distrust with regard to the accuracy of the general conclusions.[1] According to Luys, the fibres of the encephalon have several directions, as follows:

The gray matter of the cerebral hemispheres, as we shall see farther on, is composed of a mass of nerve-cells, connected together by their prolongations into a plexus, which, in its turn, is connected with the fibres of the white substance.

From this cortical cellular plexus, white fibres arise, which may be divided, according to their direction and destination, into two classes: The first class consists of curved commissural fibres, which pass into the white substance to a certain depth and return to the gray matter, connecting thus the gray substance of adjacent convolutions. The existence of these fibres and their direction are well established. The second class consists of fibres which, arising from the gray substance of the convolutions, connect these with the corpora striata and the optic thalami. These may be called the converging fibres; and their general direction, as far as it has been ascertained, is as follows:

Arising from the internal, concave surface of the cortical substance of the cerebrum, the converging fibres, at first running side by side with the curved commissural fibres, separate from the latter as they curve backward to pass again to the cortical substance, and are directed toward the corpora striata and the optic thalami. The limits of the irregular planes of separation of the commissural and the converging fibres contribute to form the boundaries of the ventricular cavities of the brain. If we study the course of the converging fibres arising from all points in the concave surface of the cerebral gray matter, we find that they take various directions. The fibres from the anterior region of the cerebrum pass backward, and form distinct fasciculi

[1] Luys, *Recherches sur le système nerveux cérébro-spinal, sa structure, ses fonctions et ses maladies*, Paris, 1865.

which converge to the gray substance of the corpora striata. The fibres from the middle portion converge regularly to the middle region of the external portions of the optic thalami. The fibres from the posterior portion pass from behind forward, and distribute themselves in the posterior portion of the optic thalami. The fibres from the convolutions of the hippocampi and the fascia dentata are lost in the gray substance lining the internal borders of the optic thalami. In addition to these converging fibres and the curved commissural fibres connecting the different convolutions of each hemisphere with each other, are commissural fibres which connect the two hemispheres, as well as fibres connecting together the corpora striata and the optic thalami of the two sides.

Certain of the fibres converging from the gray substance of the hemispheres to the corpora striata and optic thalami are probably connected with the cells in the gray matter of these parts. Other fibres pass through the corpora striata and optic thalami to become finally connected with the fibres of the medulla oblongata, and, through the medulla oblongata, with the columns of the spinal cord. Following the antero-lateral columns of the cord from below upward, they ascend to the medulla oblongata, decussate in the median line, and from the medulla pass to the brain. Certain of these ascending fibres, which are nearly all continuations of the antero-lateral columns of the cord, ascend to the brain by passing deeply through the pons Varolii; other fibres ascend in the cerebral peduncles, or crura cerebri; and other fibres pass to the tubercula quadrigemina. As the bundles of fibres ascend from the medulla oblongata, they become more and more numerous by reënforcements of fibres, probably derived from the cells of the collections of gray matter in their course.

We have attempted, in the above sketch of the fibres of the brain, to give a succinct account of the points that are most interesting from their physiological relations, and to

confine our description, as far as possible, to anatomical facts that have been definitively settled and are now generally accepted. But, as we have before remarked, the course of the fibres and their connections are so exceedingly intricate, that we cannot rely entirely upon purely anatomical investigations. The results obtained by anatomists should be controlled, as far as possible, by physiological and pathological observations. When anatomical researches are directly opposed to the conclusions to be deduced from experiments upon living animals, in view of the great uncertainty of the former, it will generally be reasonable to assume that they are erroneous or incomplete. We know, as the results of experiments on animals, that the motor stimulus is conducted from the brain by the antero-lateral columns of the cord, and that the conducting fibres decussate at the medulla oblongata. This fact has been verified by pathological observations, chiefly in cases of injury to the brain-substance from hæmorrhage, softening, etc. We know that impressions are appreciated as sensations in some part of the cerebrum, and that the sensory conductors also decussate; as is shown by occasional paralysis of both motion and sensation following brain-lesions. It is evident, therefore, that sensory conductors pass to the brain, but their precise course is not easy to determine. We have seen, in treating of the action of the cord as a conductor, that sensory impressions are transmitted by the gray substance alone, and it is probably through connections between the cells of the different centres that these impressions are finally carried to the brain. The physiological fact of the conduction of sensory impressions is fully confirmed by pathology, but its mechanism has been very little, if at all, elucidated by anatomical researches.

We have left certain anatomical points relating to the cerebrum, cerebellum, tuber annulare, and medulla oblongata, to be described separately in connection with these divisions of the encephalon.

The Cerebrum.

The anatomical description which we have just given of the encephalon will answer for most of the points of physiological interest connected with the cerebrum. As we have seen, the cerebrum constitutes more than four-fifths of the encephalic mass. Its gray matter, which is external and follows the convolutions, is from $\frac{1}{12}$ to $\frac{1}{8}$ of an inch in thickness.[1] Writers have described this substance as existing in several layers, but this division is mainly artificial. In certain parts, however, particularly in the posterior portion of the cerebrum, the gray substance is quite distinctly divided into two layers, by a very delicate intermediate layer of a whitish color.

There is a marked difference in the appearance of the cells in the most superficial and in the deepest portions of the gray substance. The superficial cells are small, and present a net-work of delicate, anastomosing fibres, resembling the cells of the posterior cornua of the gray substance of the cord; while the deepest cells are large, and resemble the so-called motor cells of the cord. Between these two extremes, in the intermediate layers, there is a gradual transition in the size of the cells.[2] This anatomical fact points to the possibility of distinct functions of the cells belonging to the superficial and the deep layers; viz., that the larger cells are for the generation of the motor stimulus, while the smaller are for the reception of sensory impressions. This, however, is mere supposition, incapable, as yet, of positive demonstration.

[1] LUYS, *Système nerveux*, Paris, 1865, p. 161.

[2] The above general description of the peculiarities of the nerve-cells of the cerebral convolutions is the one given by most anatomists. Lately, Lockhart Clark has described the structure of the convolutions very minutely, dividing the gray substance into seven distinct layers. This description is interesting, but chiefly so from an anatomical point of view. (LOCKHART CLARK, *The Structure of the Cerebral Convolutions.—Quarterly Journal of Psychological Medicine*, New York, 1869, vol. iii., p. 517.)

The mode of connection between the cellular and the fibrous elements of the nervous system has already been considered, and does not demand further mention.[1] We will also pass over the amorphous matter, nuclei, myelocytes, etc., found in the central nervous matter, as these points possess little or no physiological interest.

General Properties of the Cerebrum.—By the general properties of the cerebrum, we mean the effect, or the absence of effect, observed when the gray or white substance is subjected to direct irritation. While some of the older writers state that the brain is both irritable and sensible,[2] nearly all authorities, up to a very recent date, are agreed that direct stimulation of the white or the gray substance of the greatest part of the brain produces neither pain nor convulsive movements. Among the numerous experimenters who have exposed the brain and noted the absence of pain and convulsions after direct stimulation of both the gray and the white matter, may be mentioned Flourens,[3] Magendie,[4] and Longet. Longet states that he has exposed the cerebrum in goats, and irritated both the white and the gray substance by laceration, cauterization with potash and nitric acid, the galvanic current, etc., with purely negative results.[5] In numerous experiments upon pigeons, we have invariably observed the same insensibility and inexcitability of both the gray and the white substance of the cerebral hemispheres.

[1] See page 50.

[2] The most definite experiments on this point are those made by Haller and Zinn, these observers noting, as it seemed to them, indications of pain, and convulsive movements, immediately following mechanical irritation of the brain. (Haller, *Mémoires sur la nature sensible et irritable des parties du corps animal*, Lausanne, 1756, p. 201, *et seq.*)

[3] Flourens, *Système nerveux*, Paris, 1842, p. 18.

[4] Magendie, *Leçons sur les fonctions et les maladies du système nerveux*, Paris, 1841, tome i., p. 175, *et seq.*

[5] Longet, *Anatomie et physiologie du système nerveux*, Paris, 1842, tome i., pp. 642, 644.

From the above facts, all physiologists of the present day are agreed that a great part of the substance of the cerebrum is neither excitable nor sensible, in the sense in which these terms are applied to the ordinary mixed nerves. There can be no doubt with regard to the conducting properties of the white matter of the brain, but the nerve-fibres here seem to conduct impressions conveyed to them by the sensory nerves and the stimulus generated by the nerve-cells, without being capable of receiving or conducting artificial impressions applied directly to their substance.

We have said that a great part of the cerebral substance seems to be neither excitable nor sensible to direct stimulation; but we must make an exception in favor of certain portions of the cerebrum, which have lately been shown to possess excitability, their action being confined to particular sets of muscles. Fritsch and Hitzig, exposing the cerebral hemispheres in dogs, found that certain parts of its anterior portion responded to a feeble galvanic current. The stimulation was applied by means of two needles, conducting a feeble galvanic current, introduced through the gray into the white substance. Each galvanization produced movements restricted to particular sets of muscles; but it was difficult to say whether the contractions were due to stimulation of the white or of the gray substance. Different centres for the sets of muscles were accurately determined. The centre for the muscles of the neck was located in the middle of the frontal convolution; external to that, was a centre for the extensor and adductor muscles of the forelegs; and so on, other centres for sets of muscles being found in the anterior portion of the hemispheres. By passing an interrupted current through these parts, tetanus of particular muscles was produced. In other observations, when the gray substance was removed at the points mentioned, there was partial loss of power, but not paralysis, of the sets of muscles corresponding to the centres operated upon. The authors regarded this as due to a loss of "muscular sense." In these experi-

ments, the action was always crossed. It was also found that, after severe hæmorrhage, the excitability of the cerebrum quickly disappeared, which may account for the negative results obtained by previous experimenters. No motor properties were found in the posterior portion of the cerebrum.[1]

The experiments just cited throw a new light upon the properties of the cerebral substance. It has always been found difficult to experiment upon the great encephalic centres without disturbing the physiological conditions so seriously as to render the results of direct observations of this kind more or less indefinite. Now that it is ascertained that, in all probability, these centres readily lose their normal properties as a simple consequence of hæmorrhage and exposure of the parts, we are less disposed to accept the older experiments, in which the cerebral tissue was apparently shown to be incapable of receiving direct artificial impressions. There can be scarcely any doubt with regard to the positive results obtained by Fritsch and Hitzig; and it is by no means improbable that further investigations may show that other parts of this centre are excitable. For the present, we can only accept the definite conclusions drawn by these physiologists from their direct experiments, admitting that we are prepared to learn, from further observations, that other parts have analogous properties.

Functions of the Cerebrum.

The history of the functions of the encephalon belongs without question to physiology, and is one of the most exten-

[1] FRITSCH UND HITZIG, *Ueber die electrische Erregbarkeit des Grosshirns.—Archiv für Anatomie, Physiologie, und wissenschaftliche Medicin*, Leipzig, 1870, S. 300, *et seq.*

In the *London Lancet*, October 21, 1871, No. xvii., p. 581, is a note stating that the experiments of Fritsch and Hitzig have been confirmed by Schiff. Schiff is of the opinion, however, that the movements produced by stimulation of the brain-substance do not depend upon direct excitability of the brain, but are reflex, the result of irritation of parts concerned in tactile sensibility. As far as we know, the experiments of Schiff have not yet been published in full.

sive and interesting of the subdivisions of the science; but its range is so extensive, that it has long been regarded as a science by itself, and is only treated of exhaustively in special treatises on psychology. The study of psychology has been pursued by the method of observation much more than by direct experiment. It comprehends, it is true, the facts deduced from experiments upon living animals, but the results obtained by this method are comparatively few and their scope is restricted. Nevertheless, they are sufficiently definite; and if these results be corrected and applied to the human subject by a comparison with pathological facts, there still remains in psychology much that may be regarded as within the range of experimental physiology; for pathological cases are very frequently available to the physiologist as accidental experiments indicating the functions of parts of the human organism. We cannot restrict ourselves, however, to this method in the study of the intellectual phenomena; and must draw upon facts in comparative anatomy and physiology, anthropology, and, finally, upon the direct observation and classification of the intellectual processes.

The experimental physiologist has shown that the encephalon may receive impressions and appreciate them as sensations; that impressions may be here connected and give rise to various of the phenomena of animal and intellectual existence; that impressions are recorded by the memory; and, finally, that certain parts are endowed with special functions. But beyond this, psychology is a science mainly of introspective observation; the facts contributed by the experimentalist being few and barren. The observer of intellectual phenomena studies the process of development of the mind. He soon separates the instinctive phenomena, observed in the lower animals, and in the human being without experience, from the acts which follow experience, observation, the recording of impressions by memory, and the generation of ideas. He brings his perfected intelligence to bear upon the process of development of the same kind of intelligence

in the human being progressing from infancy to adult life; and finally, the psychological philosopher attempts, by introspective observation, to study the workings of the perfect intellect, his only means of investigation being the very intelligence he is endeavoring to comprehend.

If it were possible to bring to bear upon speculative philosophy the same positive methods employed with success in most of the natural sciences, the results of the study of the mind would be much more definite; for we would then be able to eliminate much that is purely hypothetical, resting on no established basis in fact. As we are studying the mind itself with the mind, and as many psychologists endeavor to submit their ideas to the test of personal experience, it is necessary that the investigator should be entirely free from the disturbing elements of intellectual inaccuracy or unjustifiable prejudice; but, unfortunately, the effects of early impressions made by faulty education are not often entirely removable; and notions that apparently can never be supported by facts are apt to take the place of sound philosophic reasoning. Ideas of this kind might, perhaps, be rationally entertained and discussed at a period when our positive physiological knowledge amounted to almost nothing, as before the discovery of the circulation, when our literature was filled with disquisitions upon the generation of the "*spiritus*," the location of the passions, etc.; but as knowledge has advanced and as established facts are more and more numerous and available in the study of mental phenomena, the range of pure speculation should become more and more restricted.[1]

At the present day, we are in possession of a sufficient number of positive facts to render it certain that there is and can

[1] A striking example of rapid advance from the most vague and absurd mysticism toward positive physiological knowledge is afforded by a comparison of the "*Œconomia Regni Animalis*," written by Swedenborg, one of the most learned men of his day, in the middle of the eighteenth century, with the great work by Haller (*Elementa Physiologiæ*), published only a few years later.

be no intelligence without brain-substance; that when brain-substance exists in a normal condition, intellectual phenomena are manifested, with a vigor proportionate to the amount of matter existing; that destruction of brain-substance produces loss of intellectual power; and finally, that exercise of the intellectual faculties involves a physiological destruction of nervous substance, necessitating regeneration by nutrition, here, as in other tissues in the living organism. The brain is not, strictly speaking, the organ of the mind, for this statement would imply that the mind exists as a force, independently of the brain; but the mind is produced by the brain-substance; and intellectual force, if we may term the intellect a force, can be produced only by the transmutation of a certain amount of matter.

In view of these facts, which have long been more or less fully recognized, though not, perhaps, very accurately defined in words until within a few years, it is not surprising that attempts have been made to locate the different mental attributes in particular portions of the brain.[1] The old pseudo-science of phrenology is the most marked example of such an attempt; but this has so slight a basis in fact, that it does not, at the present day, merit serious scientific discussion.

In treating of the functions of the cerebrum, we shall not discuss psychology, except in so far as physiologists have been able to connect the mind, taken as a whole, with a distinct division of the nervous system. In this we will draw upon experiments on living animals, facts in comparative

[1] Gall, whose labors have hardly received proper consideration at the hands of many physiological writers, from the fact that he is regarded as the founder of the untenable system of phrenology, is entitled to the credit of having immensely advanced our knowledge of the anatomy of the brain; but unfortunately, his visionary and unsupported theories overshadowed his merits as an exact anatomical investigator. As we do not enter into the early history of anatomical researches, we have not referred before to his great work in six volumes, which contains a large number of important facts, novel and interesting at the time of its publication. (GALL, *Sur les fonctions du cerveau et sur celles de chacune de ses parties*, Paris, 1822–'25.)

physiology, in pathology, and, to a certain extent, the relations clearly shown to exist between the development of intelligence and certain of the nerve-centres, in different races of men and different individuals. With regard to the location of particular functions in distinct portions of the cerebrum, we have but little definite knowledge, beyond the experiments already cited in treating of the irritability of the cerebral substance, and the probable location of the faculty of speech. The latter point will be fully discussed in its appropriate place.

Extirpation of the Cerebrum in Animals.—It is, perhaps, sufficiently evident, from anthropological and pathological observations, as well as the study of comparative physiology, that the intellectual faculties reside in the encephalon; but these methods of investigation do not clearly indicate the special functions of different parts of the cranial contents. We have seen, in our general sketch of the anatomy of the brain, that this is by no means a simple organ, and that certain parts, though they are bound together by commissural fibres, have sufficient anatomical distinctness to lead the physiologist to suppose that they have separate and peculiar properties and functions. One of the most valuable methods of investigation of the functions of these separate ganglia is that of extirpation of one or more, leaving the others, as far as possible, intact. This method was first employed with marked success by Flourens, and has since been adopted by numerous experimenters. It must be remembered, however, that there is no subject of physiological inquiry in which it is so difficult to apply experiments on the inferior animals to the human subject, and none in which the results of experiments should be received with greater caution. The reason for this is apparent enough. The brain and the intellectual power of man are so far superior to the development of this organ and its properties in the lower animals, that some philosophers have regarded the human intelligence as distinct

in nature as well as in amount. Although we are by no means prepared to accept this proposition, regarding, as we must, the intelligence of man as simply superior in development to that of the lower animals, it is evident that this difference in the degree of development is so enormous as to render the human mind hardly comparable with the intellectual attributes of animals low in the scale. But when the human brain is slightly developed, as in idiots, or when the intellectual faculties are simply diminished in activity, as in certain cases of disease, the being is reduced to a condition very like that of some of the lower animals.

Experiments upon different classes of animals show clearly that the brain is less important, as regards the ordinary manifestations of animal life, in proportion as its relative development is smaller. For example: if we remove the cerebral hemispheres in fishes or reptiles, the movements which we call voluntary may be but little affected; while, if the same mutilation be performed in birds or some of the mammalia, the diminished power of voluntary motion is much more marked. It would be plainly unphilosophic to assume, because a fish or a frog will swim in water and execute movements after removal of the hemispheres, very like those of the uninjured animal, that the feeble intelligence possessed by these animals is not destroyed by the operation. It is not only possible, but probable, that in the very lowest of the vertebrates, the functions of the nervous centres are not the same as in higher animals. There is, for example, a fish (the lancet-fish, *Amphioxus lanceolatus*), that has no brain, all of the functions of animal life being regulated by the gray substance of the spinal cord.[1] It is essential, in endeavoring to apply the results of experiments upon the brain in the lower animals to human physiology, to isolate, as far as possible, the distinct manifestations of intelli-

[1] MEYNERT, in STRICKER, *Handbuch der Lehre von den Geweben*, Leipzig, 1868, S. 695; and, VAN DER HOEVEN, *Handbook of Zoology*, Cambridge, 1858, vol. ii., p. 56.

gence, from automatic movements. Bearing in mind, then, the difficulties of the question and the caution with which all observations upon the great nerve-centres of the lower animals must be received in their applications to pure human physiology, we will proceed to discuss the phenomena following removal or injury of the cerebrum in direct experiments.

In 1822 and 1823, Flourens communicated to the French Academy of Sciences his remarkable observations upon the different parts composing the encephalon. His experiments are so familiar to physiologists, that it is only necessary here to give his general conclusions. As regards the cerebral hemispheres, he found that the complete removal of these parts in living animals, frogs, pigeons, fowls, mice, moles, cats, and dogs, was invariably followed by stupor, apparent loss of intelligence, and absence even of the ordinary instinctive acts. Animals thus mutilated retained general sensibility and the power of voluntary movements, but were thought to be deprived of the special senses of sight, hearing, smell, and taste. As regards general sensibility and voluntary movements, Flourens was of the opinion that animals deprived of their cerebral lobes possessed sensation, but had lost the power of perception, and that they could execute voluntary movements when an irritation was applied to any part, but had lost the power of making such movements in obedience to a spontaneous effort of the will. One of the most remarkable phenomena observed was entire loss of memory and the power of connecting ideas. The voluntary muscular system was enfeebled, but not paralyzed. Removal of one hemisphere produced, in the higher classes of animals experimented upon, enfeeblement of the muscles upon the opposite side, but the intellectual faculties were in part or entirely retained. Removal of even a considerable portion of both hemispheres was followed by no very marked effect as regards the intelligence.[1]

[1] Flourens, *Recherches expérimentales sur les propriétés et les fonctions du système nerveux*, Paris, 1842, pp. 18, 31, 98, etc.

The observations of Flourens have been repeated by numerous experimentalists, and were, in the main, confirmed, except as regards the special senses. Bouillaud, in 1826, made a large number of observations on pigeons, fowls, rabbits, etc., in which, after removal of the hemispheres, he noted the persistence of the senses of sight and hearing.[1] Longet finally demonstrated the fact that both sight and hearing are retained after extirpation of the hemispheres, even more clearly than Bouillaud, by the following experiments: He removed the hemispheres from a pigeon, the animal surviving the operation eighteen days. When this animal was placed in a dark room and a light was suddenly brought near the eyes, the iris contracted and the animal winked; "but it was remarkable, that when a lighted candle was moved in a circle, and at a sufficient distance, so that there should be no sensation of heat, the pigeon executed an analogous movement with the head." An examination after death showed that the removal of the cerebrum had been complete. An animal deprived of the hemispheres also opened the eyes at the report of a pistol, and gave other evidence that the sense of hearing was retained.[2]

With regard to the senses of smell and taste, it is more difficult to determine their presence than to ascertain that the senses of sight and hearing are retained. It is probable, however, that the sense of smell is not abolished, if the hemispheres be carefully removed, leaving the olfactory ganglia intact; and there is no direct evidence that extirpation of the cerebrum affects the sense of taste; indeed, in young cats and dogs, Longet has noted evidences of a disagreeable impression following the introduction of a concentrated solution of colocynth into the mouth, as distinctly as in the same animals in a normal condition.[3]

[1] BOUILLAUD, *Recherches expérimentales sur les fonctions du cerveau.—Journal de physiologie*, Paris, 1830, tome x., p. 36, *et seq.*

[2] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., pp. 328, 329.

[3] *Op. cit.*, p. 430.

We will now proceed to describe, as accurately as possible, the condition of an animal after complete extirpation of the cerebrum, as observed in numerous experiments that we have ourselves made on this subject, premising the statement that these are merely repetitions of observations made by other physiologists.

A pigeon, in a perfectly normal condition, is deprived of the hemispheres, by removing the calvarium and carefully scooping out the parts with the handle of a scalpel. This operation is usually not difficult, and the hæmorrhage is soon arrested spontaneously. The slit in the scalp is closed with sutures, and the animal is set at liberty.

The appearance of the animal after this mutilation is peculiar and characteristic. There immediately supervenes a condition of stupor. There is usually no attempt at movement, and, though the pigeon stands upon its feet, the head is almost buried in the feathers of the neck, the eyes are closed, and the attitude is one of absolute indifference to surrounding conditions. The muscles seem to act with just sufficient vigor to maintain the standing position. If we pinch one of the toes, or grasp the beak, there is evident sensation, and a persistent and more or less vigorous effort is made to release the part. It is sufficiently evident, from these and other tests, that sensation and the power of voluntary motion are retained; but as soon as the animal is left quiet, it relapses into its stupid condition, makes no effort to escape, and apparently loses immediately all recollection of having been disturbed. The irritation has evidently produced a sensation of discomfort, and has given rise to a voluntary muscular effort; but there has been no idea of danger, nor an intelligent effort to avoid a repetition of the disagreeable or painful impression.

It is easy to demonstrate, by experiments such as we have just alluded to, that the animal sees and hears, and retains the sense of taste; but it connects no idea with any thing seen, and the report of a pistol, which, under natural

conditions, would excite terror and an idea of danger, simply causes the pigeon to give evidence that the sound has been heard. As we have already stated, it is probable that the animal has the sense of smell, but it is difficult, if not impossible, to establish this point experimentally. The same remark applies to the sensations of hunger and thirst. The animal may feel the want of water and food, but it has no idea of relieving these sensations by drinking and eating, and, if left to itself, will die of inanition.

There has been a great deal of discussion among experimentalists with regard to spontaneous voluntary movements in animals deprived of the cerebral hemispheres. The experimental conditions necessary for determining this point are the following: The observer must be certain that the removal of the hemispheres has been complete; for it has been clearly shown that even when a small amount of cerebral substance has escaped, the functions of these lobes are not entirely abolished. Again, we must be equally certain that movements which seem to be due to a spontaneous act of volition take place when the animal has not been aroused from the condition of stupor which results from the operation. Generally, when the animal is left to itself, the condition of stupor persists; but when aroused by artificial means, it will walk a few steps, plume the feathers, shake its head, and make various voluntary movements without further irritation, soon relapsing, however, into somnolency. One of the most accurate and reliable of the recent observers of these phenomena, Vulpian, asserts without reserve, that an animal, deprived completely of the cerebral hemispheres, is incapable of a spontaneous voluntary effort; and we are inclined to an unqualified adoption of this opinion. With regard to a rabbit, from which Vulpian had removed the cerebral hemispheres and the corpora striata, he makes the following statement: "I do not hesitate to say that this rabbit is completely deprived of spontaneous volition. All its movements, which are, indeed, much less varied than

those of a bird operated on in the same manner, are exclusively and directly due to a stimulation produced by exterior excitations, or by interior inclinations, such as fatigue, etc."[1]

In view of the very great variety of movements that occur in animals after removal of the cerebrum, it is quite difficult to define precisely what movements are due to voluntary action depending upon some external or interior impression, which are really reflex voluntary movements, and to distinguish them from those which arise from a spontaneous and, perhaps, an intelligent effort of the will. These points have been so admirably described in a recent article, by Onimus, that we quote his concluding summary:

"As a summary, in the inferior animals, as in the superior animals, the removal of the cerebral hemispheres does not cause to disappear any of the movements that previously existed. Only, these movements assume certain peculiar characters. In the first place, they are more regular, they have the true normal type, for no psychical influence intervenes to modify them; the locomotor apparatus is brought into action without interferences, and one could almost say that the *ensemble* of movements is then more normal than in the normal condition.

"In the second place, the movements executed take place inevitably after certain excitations. *It is a necessity* that the frog placed in water should swim, and that the pigeon thrown into the air should fly. The physiologist can then, at will, in an animal without the brain, determine such and such an act, limit it, arrest it; he can anticipate the movements and affirm in advance that they will take place under certain conditions, absolutely as the chemist knows in advance the reactions that he will obtain in mixing certain bodies.

"Another peculiarity in the movements that take place, when the cerebral lobes are removed, is their continuation

[1] VULPIAN, *Système nerveux*, Paris, 1866, p. 680.

after a first impression. On the ground, a frog without the brain when irritated makes, in general, two or three jumps at the most; it is rare that it makes but one. Placed in water, it continues the movement of natation until it meets with an obstacle; it is the same in the carp, eel, etc. The pigeon continues to fly, the duck and goose continue to swim, etc. We should say that there is a spring which needs for its action a first impulsion, and which is stopped by the slightest resistance. But, what is striking, is precisely that continuation of the condition once determined, and we cannot refrain from connecting the facts observed in an animal deprived of the cerebral lobes with those which constitute the characteristic properties of inorganic matter. Brought into movement, the animal without a brain retains the movement until there is exhaustion of the conditions of movement, or until it meets with resistance; taken in repose, it remains in the state of inertia until an exterior cause intervenes to bring it out of this condition. It is *living, inert matter.*" [1]

There is now no room for discussion with regard to the persistence of general sensibility after removal of the hemispheres. The experiment upon a pigeon leaves no doubt upon this point; but the susceptibility to pain has been much more strikingly illustrated in other animals. Vulpian, in describing the condition of animals operated upon in this way, illustrates the persistence of sensibility in rats and rabbits, by the violent cries which follow painful impressions.[2]

In concluding our consideration of the observations upon inferior animals, it only remains for us to discuss briefly certain late experiments, which have attracted a great deal of attention, from the fact that they seem to show that spontaneous volition exists after complete extirpation of the cerebrum. These experiments have been most ably and satis-

[1] ONIMUS, *Recherches expérimentales sur les phénomènes consécutifs à l'ablation du cerveau.—Journal de l'anatomie*, Paris, 1870–'71, tome vii., p. 644.

[2] VULPIAN, *Système nerveux*, Paris, 1866, p. 667.

factorily analyzed by Vulpian.[1] Goltz argues, from experiments on frogs and the movements executed after extirpation of the brain, that these animals make intelligent muscular efforts when deprived of the hemispheres; and the phenomena observed after this mutilation are indeed very curious. As was shown by Vulpian, in his own experiments, frogs and fishes thrown into water will swim about and the frogs will even succeed in getting out of the water, but then they immediately relapse into a torpid condition. We do not conceive that these facts are in opposition to the statement just made with regard to the absence of spontaneous volition in birds and the mammalia, particularly in view of the slight importance of the functions of the cerebrum as compared with the spinal cord in the lower orders of vertebrate animals. The views lately advanced by Voit are based upon an isolated experiment upon a pigeon that was kept alive for five months after the cerebral lobes had been, as stated by Voit, completely removed. At first the pigeon presented the phenomena usually observed after this operation; but it gradually recovered, until finally it seemed entirely normal, with the single exception that it never would eat, all food being introduced forcibly. Five months after the operation, the pigeon was killed and the encephalic cavity was found filled with a white substance containing dark-bordered nerve-fibres and nerve-cells. Voit never before observed any thing like regeneration of the nervous substance or so complete a restoration of the cerebral functions; and he regarded this as an instance of anatomical and physiological regeneration of the hemispheres. The objections to accepting this observation with the physiological conclusions presented by Voit are, that it is not only possible but probable, that the hemispheres were not entirely removed, and that the posterior portion of the encephalon had advanced to occupy in part the space originally filled by the extirpated mass.[2] While

[1] *Archives de physiologie*, Paris, 1869, tome ii., p. 301.

[2] Goltz, *Contributions à l'étude des fonctions du cerveau de la grenouille;*

we do not assume that anatomical and functional regeneration of the cerebrum in a pigeon is impossible, it must be admitted that such an extraordinary statement as that made by Voit cannot be accepted without reserve, upon the basis of a single observation.[1]

Pathological Facts bearing upon the Functions of the Cerebrum.—A careful study of the phenomena which attend certain pathological conditions of the brain in the human subject, such as laceration or pressure from effusion of blood, softening of the nervous substance, etc., taken in connection with the results of experiments upon living animals, throws considerable light upon the functions of certain distinct portions of the encephalon. Cerebral hæmorrhage very commonly involves the corpus striatum, either directly or indirectly, and then we have paralysis of motion limited to the side of the body opposite to the lesion. When the optic thalamus is affected, there is impairment of sensibility upon the opposite half of the body. These facts illustrate the course of the motor and sensory conductors from and to the cerebrum. It is not very common to observe lesions confined to the gray or white substance of the hemispheres, but when this occurs, and when there is no pressure upon the corpora striata or optic thalami, there is no paralysis of motion or sensation, though there may be a certain amount of weakness of the muscles upon the side of the body opposite to the injury. Experiments upon the inferior animals have

ROSENTHAL, *Sur les mouvements qui ont lieu après l'ablation des hémisphères cérébraux ; Sur un pigeon auquel le professeur Voit avait enlévé les hémisphères cérébraux dans le mois de juillet* 1861 ; VOIT, *Observations sur l'ablation des hémisphères cérébraux chez le pigeon.—Archives de physiologie*, Paris, 1869, tome ii., p. 301.

[1] VOIT, *Phénomènes qui suivent l'ablation des hémisphères du cerveau chez les pigeons.—Revue des cours scientifiques*, Paris, 1868–1869, tome vi., p. 256.

This observation has already been detailed in full, in connection with the question of the possible regeneration of the nerve-centres after extirpation. (See page 63.)

confirmed the conclusions to be drawn from these pathological facts. In frogs, fishes, and birds, when one hemisphere has been removed, the evidences of feebleness of the muscles of the opposite side are not very marked; but they are quite distinct in the adult mammalia. Vulpian noted, in experiments upon dogs, that the destruction of a portion of one cerebral hemisphere produced feebleness, but a very incomplete paralysis of motion upon the opposite side.[1]

It is a fact now generally admitted in pathology, that loss of cerebral substance from repeated hæmorrhage is sooner or later followed by impairment of the intellectual faculties. This point it is frequently difficult to determine in a single instance, but an analysis of a sufficient number of cases shows impaired memory, tardy, inaccurate, and feeble connection of ideas, abnormal irritability of temper, with a childish susceptibility to petty or imaginary annoyances, easily-excited emotional manifestations, and a variety of phenomena denoting abnormally feeble intellectual power, following any considerable loss of cerebral substance. In short, pathological conditions of the brain all go to show that the intellectual faculties reside in the cerebral hemispheres.

As a final argument drawn from pathology, in favor of the view just stated, we have only to allude to the size of the brain in certain cases of idiocy. Prof. Hammond, in his admirable work on "Diseases of the Nervous System," has cited several examinations of the brain in idiots, in which this organ has been found to be less than one-half of the ordinary weight; as the cases reported by Tiedemann, of $19\frac{3}{4}$, $25\frac{3}{4}$, and $22\frac{1}{2}$ ounces, in three idiots, whose ages were, respectively, sixteen, forty, and fifty years.[2] A case was reported by Mr. Gore, of an idiotic woman, forty-two years of age, whose brain weighed ten ounces and five grains;[3]

[1] Vulpian, *Système nerveux*, Paris, 1866, p. 677.

[2] Hammond, *Diseases of the Nervous System*, New York, 1871, p. 326.

[3] Gore, *Notice of a case of Micro-cephaly.—Anthropological Review*, London, 1863, No. i., p. 170.

and one is reported by Mr. Marshall, of an idiotic boy, twelve years old, whose brain weighed but 8½ ounces.[1] Mr. Bradley, in a late number of the *Journal of Anatomy and Physiology*, gives an elaborate description of the brain of an idiot, thirty-five years of age, extremely emaciated at the time of his death, when he weighed but sixty pounds. The encephalon, including the cerebrum, cerebellum, and pons, weighed twenty-eight ounces, and the proportion of the cerebellum to the cerebrum was as 1 to 5·5. In the healthy adult male, of ordinary weight, the encephalon weighs fifty ounces, and the proportion of the cerebellum to the cerebrum is as 1 to 8$\frac{4}{7}$. Mr. Bradley calls attention to the proportion of the cerebellum to the cerebrum in this case, stating that this is common in the encephalon of idiots.[2] In idiots, the weight of the body is generally much below the normal standard; and in the case reported by Bradley, the proportionate weight of the encephalon to that of the entire body is even greater than in the healthy adult. If, for example, we double the weight of the body and the brain, we would have, for one hundred and twenty pounds of weight, an encephalon of fifty-six ounces. This point, however, cannot be admitted as an argument against the fact that congenital idiocy is usually attended with an abnormally small development of the hemispheres. Most idiots take little or no exercise; they are under-sized, and have but little muscular vigor; and it is probable that the general development of the body is more or less a consequence of the abnormal cerebral condition.

[1] MARSHALL, *Brain and Calvarium of a Microcephale.—Anthropological Review*, London, 1863, No. ii., Appendix, containing the *Transactions of the Anthropological Society of London*, p. ix.

[2] BRADLEY, *Description of the Brain of an Idiot.—Journal of Anatomy and Physiology*, Cambridge and London, 1871, vol. vi., p. 67.

Gratiolet, in an article on microcephaly, states that the development of the cerebellum, in proportion to the size of the cerebrum, is enormous, and that the reduction in the size of the encephalon is almost exclusively in the cerebral hemispheres. (*Mémoire sur la microcéphalie.—Journal de la physiologie*, Paris, 1860, tome iii., p. 115.)

We might compare the weight of the body in Mr. Bradley's case with that of a child from seven to fourteen years of age; and at this period of life, according to the tables compiled by Quain, the average weight of the encephalon is 45·96 ounces, for the male, and 40·78 ounces, for the female.[1]

The statements just made with regard to the brains of idiots refer to cases characterized by complete absence of intelligence, and furthermore, probably, by very small development of the body. On the other hand, there are instances of idiocy, the body being of ordinary size, in which the weight of the encephalon is little if any below the average. Lélut reports several cases of this kind. In one of these, a deaf-mute idiot, forty-three years of age, a little above the ordinary stature, presenting "idiocy of the lowest degree; no speech; almost no sign of intelligence; no care for cleanliness," the encephalon weighed 48·32 oz. Other cases of idiots of medium stature are given, in which the brain weighed but little less than the normal average.[2] These facts illustrate the difficulty of subordinating individual observations to any general rule, and this is particularly marked with regard to the brain, the structure of which is so complex and difficult of investigation.

Comparative Development of the Cerebrum in the Lower Animals.—It is only necessary to refer very briefly to the development of the cerebrum in the lower animals as compared with the human subject, to show the connection of the hemispheres with intelligence. In man, the cerebrum presents an immense preponderance in weight over other portions of the encephalon; and in some of the lower animals, the cerebrum is even less in weight than the cerebellum. In man, also, not only the relative but the absolute weight of the brain is greater than in lower animals, with but two exceptions. Todd cites

[1] QUAIN, *Elements of Anatomy*, London, 1867, vol. ii., p. 569.

[2] LÉLUT, *Du poids du cerveau considéré dans ses rapports avec le développement de l'intelligence.—Physiologie de la pensée*, Paris, 1862, tome ii., p. 308.

a number of observations made upon the brains of elephants, in which the weights ranged from nine to ten pounds.[1] Rudolphi gives the weight of the encephalon of a whale, seventy-five feet long, as considerably over five pounds.[2] With the exception of these animals, man possesses the largest brain in the zoological scale.

Another interesting point in this connection is the development of cerebral convolutions in certain animals, by which the relative amount of gray matter is increased. In fishes, reptiles, and birds, the surface of the hemispheres is smooth; but in many mammalia, especially in those remarkable for intelligence, the cerebrum presents a greater or less number of convolutions, as it does in the human subject.[3]

Comparing the relative size of the brain, its complexity of organization, and the increase of its gray substance by convolutions, with the development of intelligence in the animal scale, it is so evident that the cerebrum is the seat of the intellectual faculties, that this point in our argument seems to need no farther discussion.

Development of the Cerebrum in Different Races of Men and in Different Individuals.—It may be stated as a general proposition, that in the different races of men, the cerebrum is developed in proportion to their intellectual power; and in different individuals of the same race, the same general rule obtains. Still, this law presents marked exceptions. Certain brains in an inferior race may be larger than the average in the superior race; and it is frequently observed that unusual intellectual vigor is coexistent with a small brain, and the reverse. These exceptions, however, do not take away from the force of the original proposition. As

[1] Todd, *Cyclopædia of Anatomy and Physiology*, London, 1839–'47, vol. iii., p. 664, Article, *Nervous Centres.*

[2] Rudolphi, *Grundiss der Physiologie*, Berlin, 1823, Bd. ii., Erste Abtheilung, S. 12.

[3] Van der Hoeven, *Handbook of Zoology*, Cambridge, 1858, vol. ii., pp. 42, 227, 358, 596.

regards races, the rule is found invariable, when a sufficient number of observations are analyzed, and the same holds true in comparing a large number of individuals of the same race. Average men have an advantage over average women of about six ounces of cerebral substance; and, while many women are far superior in intellect to many men, such instances are not sufficiently numerous to invalidate the general law, that the greatest amount of intellectual capacity and mental vigor goes with the greatest quantity of cerebral substance. If we accept the view, which is in every way reasonable, that the gray substance of the cerebral hemispheres is the generator of the mind, it would be necessary, in comparing different individuals with the view of establishing a definite relation between brain-substance and intelligence, to estimate the amount of gray matter; but it is not easy to see how this can be done with any degree of accuracy.

It is undoubtedly true that proper training and exercise develop and increase the vigor of the intellectual faculties; and that thereby the brain is increased in power, as are the muscles, under analogous conditions. This will perhaps explain some of the exceptions above indicated; but an additional explanation may be found in differences in the quality of brain-substance in different individuals, independently of the size of the cerebral hemispheres. One evidence that these differences in the quality of intellectual working matter exist is, that some small brains actually accomplish more and better work than some large brains. This fact may be due to differences in training, to the extraordinary development in some individuals of certain qualities, to intensity and pertinacity of purpose, capacity for persistent labor in certain directions, a fortunate direction of the mental efforts, opportunity and circumstances, etc. But, aside from these considerations, there are analogies in the muscular system, which render it exceedingly probable that there are important individual differences in the quality of generating nervous matter.

We have in our mind at this moment two persons, in a condition of perfect health and muscular development, who have devoted about fifteen years to the same kind of athletic exercise, but who present the most marked differences in muscular power. One of these has an enormously-developed muscular system, the muscles being large and as hard as is ever seen. In this individual, the arm over the biceps measures seventeen inches in circumference. He can raise from the shoulder with the right hand and stand erect with the arm straight under a weight of a little less than one hundred pounds. The other individual has muscles of about the same hardness, but very much smaller. His arm measures over the biceps a little more than fourteen inches; but he can raise from the shoulder a weight of one hundred and thirty-eight pounds. A third individual can "put up" from the shoulder, a dumb-bell of the enormous weight of one hundred and eighty-one pounds. This feat we have seen executed, and have accurately verified the weight. The gentleman referred to, Mr. Richard A. Pennell, of New York, is not a professional gymnast, but is one of the strongest men, in this particular exercise, on record, certainly in this country. His height is five feet ten inches; weight, one hundred and ninety-five pounds, without clothing; his muscles are large, but rather soft. As this exhibition of muscular power is, we believe, almost unparalleled, we may state that the weight is pushed slowly and gradually from the shoulder, the arm is straightened, and the body is brought to an erect position under the weight, which is held perfectly balanced in the right hand for several seconds. Less striking examples of such differences in muscular quality are innumerable, and must have been observed by those interested in athletic exercise; and in view of this, it seems not only possible but probable, that the generating portion of the nervous system possesses analogous differences in quality in different persons.

In concluding this portion of our argument, we present a table of an exceedingly interesting series of observations

of the comparative weights of the encephalon in the Caucasian, the negro, and the intermediate grades produced by the union of the two races. The observations in this table are hardly sufficient in number to establish the exact relations between the brains in the different grades of color, but they illustrate points of peculiar interest in this country, where the blacks are so numerous, and where the union of the two races, white and black, is so common. As far as the results go, they are in decided opposition to those given by Tiedemann, in his remarkable memoir on the brain of the negro.[1]

We also give a list of some of the well-authenticated weights of the encephalon in men whose intellectual faculties had been observed during life.[2] This latter list we have prepared with great care, and have introduced some observations not found in the works on physiology. In estimating the intellectual power of individuals, it is difficult to arrive at exact conclusions, except with regard to men of acknowledged eminence. Still, the statements are as accurate as possible, and must be taken for what they are worth. Several of the examples given in this list are marked exceptions to the general rule, that the mental vigor is in proportion to the development of brain-substance.[2]

[1] TIEDEMANN, *Das Hirn des Negers*, Heidelberg, 1837.

[2] We have not considered it necessary to enter into a discussion of the relations of the facial angle to intelligence, in the lower animals and in different races of men. It was proposed by Camper to take the angle made at the junction of two lines, one drawn from the most projecting part of the forehead to the alveolæ of the teeth of the upper jaw, and another passing horizontally backward from the lower extremity of the first line, as the facial angle. This angle is, to a certain extent, a measure of the projection of the anterior lobes of the brain. Numerous observations upon the facial angle in different races were made by Camper and other physiologists and ethnologists. They show, in general terms, that the angle is larger in man than in any of the inferior animals, and is largest in those races that possess the greatest development of intellectual power. (CAMPER, *Dissertation physique sur les différences réelles que présentent les traits du visage*, etc., Autrecht, 1791. BROCA, *Sur l'angle facial et le triangle facial.—Mémoires d'anthropologie*, Paris, 1871, tome i., p. 110.)

Ethnological Table, derived from 405 Autopsies of White and Negro Brains. Made under the direction of Surgeon Ira Russell, 11th Massachusetts Volunteers.[1]

	No. of Autopsies.	Grade of Color.	Average Weight of Brain.	Maximum Weight of Brain.	Minimum Weight of Brain.	Brains, 60 oz. and over.	Brains, 55 and under 60 oz.	Brains, 50 and under 55 oz.	Brains, 45 and under 50 oz.	Brains, 40 and under 45 oz.	Brains, 35 and under 40 oz.	Brains less than 35 oz.
	24	White	52·06	64	$44\frac{1}{4}$	1	4	11	7	1	.	.
	25	$\frac{3}{4}$ "	49·05	51	40	1	.	10	12	2	.	.
	47	$\frac{1}{2}$ "	47·07	57	$37\frac{3}{4}$	.	2	13	19	12	1	.
	51	$\frac{1}{4}$ "	46·54	59	$38\frac{1}{2}$	.	2	10	22	11	6	.
	95	$\frac{1}{8}$ "	46·16	57	$34\frac{1}{2}$	.	1	15	50	21	7	1
	22	$\frac{1}{16}$ "	45·18	$50\frac{1}{2}$	40	.	.	3	10	9	.	.
	141	Black	46·96	56	$35\frac{3}{4}$	.	5	42	51	38	3	.
	405					2	14	104	171	94	17	1
Autopsies of Clendinning, Sims, Reid, and Tiedemann	278	Whites, collated from various sources	$49\frac{1}{2}$	65	34	7	28	99	97	39	7	1

Table of Weights of the Encephalon, in ounces, av., in Individuals, in some of whom the Degree of Intelligence is more or less accurately known.

1. Cromwell,[2] aged 59 (not accepted by physiologists) . . . 82·29 oz.
2. Byron,[3] aged 36 (not accepted by physiologists) . . . 79·00 "
3. Cuvier, aged 63 . . . . 64·33 "
4. Abercrombie, aged 63 . . . . 63·00 "

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[1] SANFORD B. HUNT, *The Negro as a Soldier.—Quarterly Journal of Psychological Medicine*, New York, 1867, vol. i., p. 182.

[2] Weight taken from WAGNER, *Fonctions du cerveau.—Journal de la physiologie*, Paris, 1861, tome iv., p. 556. Soemmerring (*De Corporis Humani Fabrica*, Trajecti ad Moenum, 1798, tomus iv., p. 38) states that he examined the skull of Cromwell, and thinks, from the size of the cranial cavity, that the weight of the brain ordinarily given must be inaccurate.

[3] *Dissection of Lord Byron.—Medico-Chirurgical Review*, London, 1825, vol. i. (American Reprint), p. 164. The statement is quoted from the *Gazette de santé*, 25 August, 1824, that "*the cerebrum and cerebellum weighed six medicinal pounds.*" This equals 79 oz. av., less 25 grains. This statement is made on the authority of Dr. Bruno, and is certainly inaccurate, especially as many biographers of Byron state that his head was unusually small.

5.	Ruloff, aged 53; above medium stature; executed for murder, in 1871; well versed in languages, imagining that he had discovered new and important principles in philology	59·00 oz
6.	James Fisk, Jr.,[1] aged 37; killed in New York, in 1872; illiterate, but said to possess great executive ability; notorious for colossal and unscrupulous financial speculations	58·00 "
7.	Spurzheim	55·06 "
8.	Adult man;[2] an idiot since two years of age	54·95 "
9.	Laborer,[2] aged 22; died of fracture of the pelvis	53·79 "
10.	Daniel Webster, aged 70	53·50 "
11.	Celebrated mathematician,[2] aged 54; above the ordinary stature	53·41 "
12.	Executed criminal,[3] aged 45; medium stature; of less than ordinary intelligence, and uncultivated	53·12 "
13.	Celebrated clinical professor,[2] aged 52; medium stature	52·88 "
14.	Mathematician of the first rank,[2] aged 78; medium stature	52·62 "
15.	Executed criminal,[3] aged 34; rather large in stature; ordinary intelligence, but singular, and somewhat cultivated	50·09 "
16.	Dupuytren, aged 58	49·68 "
17.	Day-laborer,[2] aged 49	48·85 "
18.	Executed criminal,[3] aged 29; medium stature; of scarcely ordinary intelligence, and uncultivated	48·81 "
19.	Executed criminal,[4] aged 42; a little above medium stature; intelligence fine, developed, and slightly cultivated	48·81 "
20.	Idiot, of a very low degree of intelligence;[4] aged 37; a little above medium stature; movements very active	48·67 "
21.	Deaf-mute,[4] aged 43; a little above medium stature; an idiot, of the lowest degree of intelligence	48·32 "
22.	Executed criminal,[4] aged 46; medium stature; of ordinary intelligence, uncultivated, but proud and vivacious	48·14 "
23.	Man, slightly imbecile,[4] aged 67; medium stature	48·14 "
24.	Man about 60 years of age[5]	48·14 "
25.	Celebrated philologist,[5] aged 54; 5 feet 7½ inches tall	47·90 "
26.	Executed criminal,[4] aged 34; small stature; intelligence developed and cultivated	47·79 "
27.	Man, about 24 years of age;[5] died of aortic insufficiency	47·69 "
28.	Day-laborer,[5] aged 51	47·44 "
29.	Man 34 years of age;[5] died of pneumonia	47·26 "

[1] This is taken from the official report of the autopsy of James Fisk, Jr., by Dr. E. T. T. Marsh, deputy coroner, on file in the office of the district attorney, in the city of New York. The cerebrum weighed 51 ounces; the cerebellum, 6 oz., and the pons, 1 oz.

[2] Wagner, *Journal de la physiologie*, Paris, 1861, tome iv., p. 558.

[3] Lélut, *Physiologie de la pensée*, Paris, 1862, tome ii., pp. 304–310.

[4] Lélut, *loc. cit.* [5] Wagner, *loc. cit.*

30. Brigand and assassin,[1] aged 32; beheaded . . . . . . 46·91 oz.
31. Idiot of the lowest degree of intelligence,[2] aged 24; medium stature 46·56 "
32. Executed criminal,[2] aged 27; medium stature; of ordinary and uncultivated intelligence . . . . 46·21 "
33. Executed criminal,[2] aged 40; at least of medium stature; intelligence developed and cultivated . . . . 46·21 "
34. Railroad laborer,[1] aged 23 . . . . 46·21 "
35. Executed criminal,[2] aged 29; intelligence hardly ordinary, and uncultivated . . . . 45·50 "
36. Wood-cutter,[1] aged 57; died of vertebral caries . . . 44·90 "
37. Idiot, below the condition of a brute;[2] aged 39 . . . 44·30 "
38. Imbecile, with difficulty in movements;[2] aged 57; intelligence correct, notwithstanding its slight development . . . 43·56 "
39. Man, 34 years of age;[1] died of phthisis . . . . . . 43·38 "
40. Celebrated mineralogist,[1] aged 77; above medium stature . . 43·24 "
41. Executed criminal,[2] aged 31; small stature; intelligence mobile and exaggerated . . . . 42·04 "
42. Upholsterer,[1] aged 60; died of phthisis . . . . . . 40·91 "
43. Imbecile,[2] aged 23; large stature . . . . 38·97 "
44. Idiot, of the lowest degree of intelligence;[2] aged 46; medium stature . . . . 36·86 "
45. Man, 46 years of age;[2] idiocy very profound; very large stature 36·15 "
46. Man, 44 years of age;[2] idiocy very profound; a little below medium stature . . . . 34·39 "

In compiling the foregoing table, we have in every instance consulted the authentic reports of the weights of the brain, and have reduced them all to ounces av. with the greatest care. This was found necessary, on account of the important variations in the reports quoted by different physiological authors, especially as regards the brains of Cuvier, Webster, and Dupuytren. We believe that our figures are absolutely correct. The weights of the brains of Cromwell and Byron are given, but there can be hardly any question that they are grossly exaggerated.

In the report of the autopsy of Cuvier, the weight of the brain is given as "*trois livres onze onces quatres gros et demi.*"[3] Cuvier died in 1832, and the weight is in the old

[1] WAGNER, *loc. cit.* [2] LÉLUT, *loc. cit.*

[3] *Note sur la maladie et la mort de G. Cuvier.—Archives générales de médecine*, Paris, 1832, tome xxix., p. 144.

poids de marc,"[1] the livre = 7,561 troy grains. The weight above given, reduced to ounces av., = 64·33.

The weight of the brain of Abercrombie is taken from the original report furnished by Dr. Adam Hunter.[2] The weight of the brain of Ruloff is taken from a full report of the autopsy in the *Psychological Journal*.[3] The weight of the brain of James Fisk, Jr., was furnished by Dr. Edward T. T. Marsh, Deputy Coroner of New York, who conducted the autopsy.[4] The weight of Spurzheim's brain was taken from the *Medico-Chirurgical Review*.[5]

The report of Daniel Webster's brain is certainly a curiosity in scientific literature. In the account of the autopsy, by Dr. Jeffries, of Boston, the actual weight of the encephalon, taken by that most accurate and reliable observer, Dr. Jeffries Wyman, was 53·5 oz. av. It is stated, however, by Dr. Jeffries, that "the weight of the brain deviated much less from the average than the measurements; it was entirely out of proportion to the unusual dimensions of the cranial cavity. . . . Both serum and lymph, there can be no doubt, encroached upon and occupied the space once filled with cerebral substance. The weight given above, therefore, cannot be regarded as being equal to the weight of the brain in a state of health." To supply this hypothetical deficiency in cerebral substance in this remarkable man, Dr. Jeffries, aided by Prof. Treadwell, of Cambridge, makes an

[1] In 1812, by a ministerial decree, the *livre* was fixed at 500 grammes, instead of 489·5 grammes, the equivalent of the *livre poids de marc;* but the old weight was generally in use in 1832, and all of the calculations, both for Cuvier and Dupuytren, are from the *poids de marc*. As far as we can ascertain, the *livre* of 500 grammes was little used, and should not be taken, unless expressly stated.

[2] *Account of the late Dr. Abercrombie.—Edinburgh Medical and Surgical Journal*, Edinburgh, 1845, vol lxiii., p. 448.

[3] Burr, *Medico-legal Notes on the Case of Edward H. Ruloff.—Journal of Psychological Medicine*, New York, 1871, vol. v., p. 738.

[4] Written communication from Dr. Marsh.

[5] *The Skull of Spurzheim.—Medico-Chirurgical Review*, London, 1836, New Series, vol. xxv. (American Reprint), p. 448.

approximative calculation, based upon the cranial capacity, the specific gravity of the brain (according to Cruveilhier, and not the actual specific gravity of the brain examined), and arrives at the conclusion that "Mr. Webster's brain will be found to rank among those whose brains are generally cited as instances of remarkable size." The brain of Cuvier is then given as weighing $64\frac{1}{3}$ oz.; Webster, $63\frac{3}{4}$ oz.; and Abercrombie, 63 oz. It is impossible to avoid the suspicion, in reading this report, that an attempt is made to make the weight of the brain accord with the acknowledged remarkable intellectual power of Mr. Webster, as well as the unusual cranial capacity.[1]

The account of Dupuytren's brain, the weight of which is often misquoted by authors, is taken from the official report of the autopsy, published in the *Revue médicale.* The encephalon weighed 2 *livres*, 14 *onces.* Taking this as *poids de marc*, the weight is 49·68 oz. av.[2]

The other weights given in the table are taken from Lélut[3] and Wagner.[4]

A careful study of the weights given in the preceding table shows the impossibility of applying to individuals an absolute rule that the greatest brain-power is connected with the greatest amount of brain-substance. The men of acknowledged intellectual ability in the table are, Cuvier, Abercrombie, Spurzheim, Webster, Dupuytren, and those cited by Wagner as celebrated mathematicians, professors, etc. Cuvier and Abercrombie stand at the head of the list, as regards the weight of the brain; but above Webster and Dupuytren, are Ruloff, Fisk, an idiot, and a common laborer. Far down in the list, is a celebrated mineralogist, whose brain is at least six ounces below the average. The ad-

[1] JOHN JEFFRIES, *An Account of the last Illness of the late Honourable Daniel Webster.—American Journal of the Medical Sciences*, Philadelphia, 1853, New Series, vol. xxv., p. 117, *et seq.*

[2] CRUVEILHIER, HUSSON, BOUILLAUD, *Procès-verbal de l'ouverture du corps de M. Dupuytren.—Revue médicale*, Paris, 1835, tome i., p. 287.

[3] *Loc. cit.* [4] *Loc. cit.*

vanced age of the person referred to, seventy-seven years, would not account for the small weight of the brain, though the weight is undoubtedly diminished in old persons. We are not surprised, then, in the tables based upon observations of thousands of healthy brains of men not remarkable for great intellect, to find many between fifty-five and sixty ounces in weight.

As the general result of all the observations upon the human subject, while we admit that intellectual vigor is in general coincident with large development of the cerebral hemispheres, there are certainly many striking exceptions to this rule when it is applied to individuals.

Location of the Faculty of Articulate Language in a Restricted Portion of the Anterior Cerebral Lobes.—Physiologists are often slow to accept important facts bearing directly upon the functions of parts, drawn exclusively from pathology, especially when these facts are not capable of demonstration by experiments upon the lower animals; and perhaps this is due to a certain distrust of the accuracy of pathological researches as compared with the exact results of well-executed experimental observations. As regards the faculty of speech, however, our study must be confined to man, the only animal capable of articulate language, and our data are drawn exclusively from pathology. Some physiological writers are still disposed to regard the location of the faculty of speech as not definitively settled; but, from a careful study of the pathology of aphasia, we are convinced that there is no point in the physiology of the brain more exactly determined than that the faculty of speech is located in a well-defined and restricted portion of the anterior lobes. This is the more interesting and important, as it is the only sharply-defined faculty that has been accurately located in a distinct portion of the brain.

We do not propose to enter fully into the history of aphasia, as this belongs to pathology. In the companion-

treatise to this volume, Hammond on the "Diseases of the Nervous System," the chapter on aphasia not only contains a full historical account of the disease, but is enriched by numerous original observations of the most striking character. The profound acquirements of Dr. Hammond as a physiologist, and his skill as an original investigator in this department, lend additional weight to his deductions. In our references to the bibliography of the subject, we shall make use of the labors of Dr. Hammond, by whom the literature has been exhaustively studied.[1]

Dr. Hammond states that "by aphasia is understood a condition produced by an affection of the brain by which the idea of language, or of its expression, is impaired." Certain cases of this disease present loss of speech because the subject is incapable of coördinating the muscles used in articulation. The patient has a clear idea of language and of the meaning of words, and is able to write perfectly well. In other cases, the patient can neither speak nor express ideas in writing. In these, the idea of language is lost. In both of these varieties of the disease, the difficulty is either in the organ presiding over the faculty of speech or in the connections of this organ with the muscles concerned in articulation. Thus regarded, aphasia does not include aphonia from laryngeal disease, or loss of speech such as is observed frequently in hysteria, in the insane, who sometimes refuse to speak from pure obstinacy, or in cases of paralysis of the parts immediately concerned in articulation. The whole history of the disease points to a particular part of the brain which presides over the faculty of speech.

While we do not propose to treat of the history of aphasia, we cannot refrain from quoting a case, detailed in 1766, by Pourfour du Petit, which possesses great historical interest, as one of the first, if not the very first, in which the symptoms now recognized as aphasic were connected with disease of the left anterior cerebral lobe. We quote this

[1] Hammond, *Diseases of the Nervous System*, New York, 1871, p. 166, *et seq.*

case in full, because it seems to have escaped the attention of writers on aphasia:

"Some time after I had made the experiments which I have just reported, a cavalryman of the garrison, aged thirty-five years, was brought into our hospital. He had been seized the day before with paralysis of the entire right side, which had occurred after a slight pleurisy, from which he had recovered; he could move neither the arm, nor the right leg, nor could he maintain himself in his seat. The lower jaw was not distorted; he opened and closed the mouth with facility. He could move the tongue only with a great deal of difficulty, and could not protrude it from the mouth, nor pronounce any word.

"The right eye seemed dimmed, and its sight was entirely lost, which I recognized, because, in presenting the finger, or a stick, very near this eye, he made no movement of the lid. But as soon as I touched the eye, he closed the lid. When I presented the finger or a stick to the left eye, he immediately closed it, though it was not touched.

"He retained sensation on the paralyzed side as well as on the sound side.

"A month after he had entered the hospital, he moved the tongue pretty easily, and even protruded it a little from the mouth, but he could pronounce nothing but *non*.

"He was attacked with scurvy fifteen days after, and with abdominal flux, from which he died two months after his entrance into the hospital, not being relieved by any remedies.

"His judgment was always perfectly normal during his disease, and he had no convulsive movements.

"After death I removed the brain and spinal cord. I began by dissecting the spinal cord, in which I found nothing abnormal, nor in the right side of the brain. But I found on the left side, the entire anterior protuberance which contains the internal and superior corpora striata (*corps cannelés*), the middle and the external or inferior, dissolved and con-

verted into a substance resembling the lees of wine. It did not appear that this part had been swollen, and that it had become larger than natural.

"Neither the optic thalami nor the optic nerves were injured."[1]

The great interest of this case will appear when we come to note the connection between aphasia and the left anterior lobe of the cerebrum.

As a preliminary to the location of the nerve-centre presiding exclusively over speech, it is necessary to establish the existence of the power of articulate language as a distinct faculty; and this is done by cases of disease in which this faculty seems to be lost, the general mental condition being unaffected. Passing over the passages in the writings of the ancients, in which it is stated that the power of speech is sometimes lost, and even some writers in the beginning of the present century, who connected this difficulty with lesions of the anterior lobes of the brain, we come to the observations of Dr. Marc Dax, who, in 1836, read a paper before the medical congress at Montpellier, in which he showed impairment or loss of speech in one hundred and forty cases of right hemiplegia. Dax concluded, from these observations, that the faculty of articulate language occupies the left anterior lobe. This memoir, however, attracted but little attention, until 1861, when the discussion was renewed by Broca; and since then, Broca, Aubertin, Charcot, Falret, Perroud, and Trousseau, have reported numerous cases of aphasia with lesion of the left anterior lobe. In 1863, M. G. Dax, a son of Marc Dax, limited the lesion to the anterior and middle part of the left anterior lobe. It was further stated, by Broca and Hughlings Jackson, to be that portion of the brain nourished by the left middle cerebral artery. This subject has been more lately investigated by Sanders, Moxon, Ogle, Bateman, Bastian, Von Benedict, Braunwart, and

[1] Pourfour du Petit, *Nouveau système du cerveau.—Recueil d'observations d'anatomie et de chirurgie*, Paris, 1766, p. 74.

by A. Flint, H. B. Wilbur, E. C. Seguin, and others, in this country. According to recent observers, the most frequent lesion in aphasia is in the parts supplied by the left middle cerebral artery, particularly the lobe of the insula, or the island of Reil; and it is a curious fact that this part is found only in man and monkeys, being in the latter very slightly developed. While we must agree with Dr. Hammond in the statement that the organ of language cannot be absolutely restricted to these parts, it is none the less certain that they are most frequently the seat of lesion in aphasia.

As illustrating the loss of the faculty of speech without any marked impairment of the intellectual faculties, we can cite numerous cases recorded by Dr. Hammond. A woman is described as presenting a countenance remarkably bright and cheerful, her whole expression being exceedingly intelligent. "She comprehends every word that is said to her, and attends to all her household duties. Yet she is unable to utter any words but 'no,' 'yes,' and 'dado.'"[1] Other cases are given, in which the intellect seemed to be clear, but in some, the faculty of speech was lost, and in others, both the faculty of speech and of writing. One case reported by Dr. Hammond is so striking that we give it in full:

"The patient was a retired officer of the army, and consulted me in the autumn of 1869 for paralysis, vertigo, and slight difficulty of speaking, from which he had suffered for some months. Several years previously he had been under the care of my friend Dr. Metcalfe, for acute rheumatism, with cardiac complications. The history of the case pointed strongly to embolism, and, as the paralysis affected the right side, I diagnosticated a previous attack of embolism of the left middle cerebral artery.

"The difficulty of speech was slight; there were both amnesic and ataxic aphasia.

"Under the treatment employed he improved very much

[1] *Op. cit.*, p. 210.

in the ability to walk, to use his arm, and to speak, so much so, that he and his friends considered him better than he had been for several years. But, about six weeks after he came under my charge, he had another attack. This time the left side was paralyzed, and there was no difficulty of speech. Galvanism was employed, as before, and he recovered sufficiently to go to Washington City. While there, he had a third attack, characterized by right hemiplegia and aphasia. He soon recovered his power of speech, and soon afterward had a further attack, involving the left side, and unattended by aphasia. He recovered under the care of Dr. Basil Norris, of the army, and soon afterward came again to New York. A short time after his arrival I requested my friend Prof. Flint to see him in consultation, with the special view of having him examine his heart. This was done with thoroughness, but no abnormal sounds were detected. While in New York he had two other attacks, during both of which he was delirious; both were characterized by hemiplegia. That of the left side was unaccompanied by aberrations of language; that of the right side was attended with ataxic and amnesic aphasia. He forgot the names of the most ordinary things, and there were many words that he could not articulate at all. Thus, when he wanted a fan, he called it 'a large, flat thing, to make wind with.' He forgot my name, and could not pronounce the words beetle, general, physician, and many others. I sent him to Newport greatly improved, but he had other attacks there, and finally died in the autumn of the present year, of, I presume, cerebral softening.

"The interesting features of this case are the concurrence of hemiplegia and ataxic and annesic aphasia, and the striking fact that there was no aphasia when the paralysis involved the left side. Thus, according to my views of the case, the patient had repeated attacks of cerebral embolism. When the embolus lodged in the left middle cerebral artery, there was aphasia accompanied by right hemiplegia; when

the embolus obstructed the right middle cerebral artery, there was left hemiplegia, but no aphasia."[1]

An analysis of a large number of cases of aphasia recorded by different observers shows that the great majority occur in connection with right hemiplegia. Dr. Hammond quotes 243 cases with right, against 17 cases with left hemiplegia. In cases verified by post-mortem examination, 514 occurred when the lesion involved the left, and 31, when it involved the right anterior lobe. Dr. Hammond cites additional cases, in 80 of which the lesion involved the left lobe, and in 2, the right lobe.

While the above facts show that the cerebral lesion in aphasia involves the left anterior lobe in the great majority of cases, there are several instances in which the right lobe alone was affected; and this has led physiologists and pathologists to deny the absolute location of the organ of language on the left side. Even if we reject a certain number of cases of aphasia with the brain-lesion limited to the right side, in which we may suppose that the post-mortem examinations were incomplete, or the impairment of speech was due, perhaps, to simple paralysis of muscles, we must admit that, in a few instances, aphasia has followed injury or disease of the brain on the right side. Aside from the anatomical arrangement of the arteries, which seem to furnish the greater amount of blood to the left hemisphere, it is evident that, as far as voluntary movements are concerned, the right hand, foot, eye, etc., are used in preference to the left; and that the motor functions of the left hemisphere are superior in activity to those of the right. It would be interesting, then, to note the physical peculiarities of persons affected with left hemiplegia and aphasia. Dr. Bateman quotes two cases of aphasia dependent upon lesion of the right side of the brain and consequent left hemiplegia, in which the persons were left-handed;[2] and these, few as they are, are interesting, as showing that a person may use the right side

[1] HAMMOND, *op. cit.*, p. 215. [2] BATEMAN, *On Aphasia*, London, 1870, p. 164.

of the brain in speech, as in the other motor functions. In this connection, it may not be uninteresting to note that, although most anatomists have failed to find any marked difference in the weight of the two cerebral hemispheres, Dr. Boyd has shown by an "examination of nearly two hundred cases at St. Marylebone, in which the hemispheres were weighed separately, that almost invariably the weight of the left exceeded that of the right by at least the eighth of an ounce."[1] To conclude our citations of pathological facts bearing upon the location in the brain of the organ of speech, we may refer to an account, by Dr. Broadbent, of the brain of a deaf and dumb woman. In this case, the brain was found to be of about the usual weight, but the left third frontal convolution was of "comparatively small size and simple character."[2]

Taking into consideration all of the pathological facts bearing upon the subject, it seems certain that, in the great majority of persons, the organ or part presiding over the faculty of articulate language is situated at or near the third frontal convolution and the island of Reil in the left anterior lobe of the cerebrum, and mainly in the parts nourished by the middle cerebral artery. In some few instances, the organ seems to be located in the corresponding part on the right side. It is possible that, originally, both sides preside over speech, and the superiority of the left lobe of the brain over the right and its more constant use by preference in right-handed persons may lead to a gradual abolition of the functions of the right side of the brain, in connection with speech, simply from disuse. This view, however, is hypothetical, but is rendered probable by certain considerations, among the most important of which is the statement by

[1] Boyd, *Table of the Weights of the Human Body and Internal Organs.—Philosophical Transactions*, London, 1861, vol. cli., part i., p. 261.

[2] Broadbent, *On the Cerebral Convolutions of a Deaf and Dumb Woman.—Journal of Anatomy and Physiology*, Cambridge and London, 1870, vol. iv., p. 225.

Longet, that "one cerebral hemisphere in a healthy condition may suffice for the exercise of intelligence and the external senses." In support of this statement, Longet cites several cases of serious injury of one hemisphere without impairment of the intellect.[1]

Another very important point, which we believe had never before been noted, is brought forward very strongly by Dr. Hammond. In what is called the ataxic form of aphasia, the idea and memory of words are intact, and there is simply loss of speech from inability to coördinate the muscles concerned in articulate language. Patients affected in this way cannot speak, but can write with ease and correctness. In the amnesic form of the disease, the idea and memory of language are lost; patients cannot speak, and are affected with agraphia, or inability to write. In cases in which hemiplegia is marked, the aphasia is of the ataxic form; while in cases in which there is no hemiplegia, the aphasia is amnesic.

"The gray matter of the lobes presides over the *idea* of language, and hence over the memory of words. When it only is involved, there is no hemiplegia, and there is no difficulty of articulation. The trouble is altogether as regards the memory of words.

"The corpus striatum contains the fibres which come from the anterior column of the spinal cord, and is besides connected with the hemisphere. A lesion, therefore, of this ganglion, or other part of the motor tract, causes paralysis of motion on the opposite side of the body. The cases I have detailed show, without exception, that the power of coördinating the muscles of speech is directly associated with this hemiplegia. A lesion, therefore, followed by hemiplegia and ataxic aphasia, indicates the motor tract as the seat. If amnesic aphasia is also present, the hemisphere is likewise involved."[2]

[1] Longet, *Anatomie et physiologie du système nerveux*, Paris, 1842, tome i., p. 666, *et seq.*

[2] Hammond, *op. cit.*, p. 217.

CHAPTER XIII.

THE CEREBELLUM.

Some points in the physiological anatomy of the cerebellum—Course of the fibres in the cerebellum—General properties of the cerebellum—Functions of the cerebellum—Extirpation of the cerebellum in animals—Incomplete extirpation of the cerebellum—Pathological facts bearing upon the functions of the cerebellum—Andral's cases—Other cases of disease of the cerebellum—Connection of the cerebellum with the generative function—Development of the cerebellum in the lower animals—Paralysis from disease or injury of the cerebellum.

It is not necessary, in order to comprehend the functions of the cerebellum, as far as these are known, to enter into a full description of its anatomical characters. The points, in this connection, that are most interesting to us as physiologists are, the division of the substance of the cerebellum into gray and white matter; the connection between the cells and fibres; the connection of the fibres with the cerebrum, and with the prolongations of the columns of the spinal cord; and the passage of fibres between the two lateral lobes. These points, therefore, will be the only ones that will engage our attention.

Some Points in the Physiological Anatomy of the Cerebellum.

As we have seen, in treating of the general arrangement of the encephalon, the cerebellum, situated beneath the posterior lobes of the cerebrum, weighs about 5·20 ounces av. in the male, and 4·70 ounces in the female. The propor-

tionate weight to that of the cerebrum is as 1 to $8\frac{4}{7}$ in the male, and as 1 to $8\frac{1}{4}$ in the female. It is separated from the cerebrum by a strong process of the dura mater, called the tentorium. Like the cerebrum, the cerebellum presents an external layer of gray matter, the interior being formed of white, or fibrous nerve-tissue. The amount of the gray substance is very much increased by numerous fine convolutions, and is farther extended by the penetration, from the surface, of arborescent processes of gray matter. Near the centre of each lateral lobe, embedded in the white substance, is an irregularly dentated mass of cellular matter, called the corpus dentatum. The cerebellar convolutions are more numerous, and the gray substance is deeper, than in the cerebrum ; and these convolutions are present in many of the inferior animals in which the surface of the cerebrum is smooth.

The cerebellum consists of two lateral hemispheres, more largely developed in man than in the inferior animals, and a median lobe. The hemispheres are subdivided into smaller lobes, which it is unnecessary to describe. Beneath the cerebellum, bounded in front and below by the medulla oblongata and pons, laterally by the superior peduncles, and superiorly by the cerebellum itself, is a lozenge-shaped cavity, called the fourth ventricle. The crura, or peduncles will be described in connection with the direction of the fibres.

The structure of the gray substance of the convolutions presents certain peculiarities. This portion is divided quite distinctly into an internal and an external layer. The internal layer presents an exceedingly delicate net-work of fine nerve-fibres, which pass to the cells of the external layer. In the plexus of anastomosing fibres, are found numerous bodies like free nuclei, called by Robin, myelocytes. The external layer is somewhat like the external layer of gray substance on the posterior lobes of the cerebrum, and is more or less sharply divided into two or more secondary

layers. The most external portion of this layer contains a few small nerve-cells and fine filaments of connective tissue; and the rest of the layer contains a great number of large cells, rounded or ovoid, with two or three, and sometimes, though rarely, four prolongations.[1] The mode of connection between the nerve-cells and the fibres has already been described under the head of the general structure of the nervous system.[2]

Course of the Fibres in the Cerebellum.—Most anatomical writers give a very simple description of the course of the nerve-fibres in the cerebellum. From the gray substance of the convolutions and their prolongations, the fibres converge to form finally the three crura, or peduncles on each side. The superior peduncles pass forward and upward to the crura cerebri and the optic thalami. These connect the cerebellum with the cerebrum. Beneath the tubercular quadrigemina, some of these fibres decussate with the corresponding fibres upon the opposite side; so that certain of the fibres of the superior peduncles pass to the corresponding side of the cerebrum, and others pass to the cerebral hemisphere of the opposite side.

The middle peduncles arise from the lateral hemispheres of the cerebellum, pass to the pons Varolii, where they decussate, connecting together the two sides of the cerebellum.

The inferior peduncles pass to the medulla oblongata, and are continuous with the restiform bodies, which, in turn, are continuations chiefly of the posterior columns of the spinal cord.

According to Luys, the fibres from the cortical substance of the cerebellum all pass to the corpora dentata and there terminate, being connected with the cells. From the corpora dentata, new fibres arise, which go to form the cerebellar peduncles. Luys does not admit the existence of com-

[1] KÖLLIKER, *Éléments d'histologie humaine*, Paris, 1868, p. 387, *et seq.*

[2] See page 50.

missural fibres connecting the two lateral halves of the cerebellum, and assumes that the decussation between the two sides takes place through a special system of decussating prolongations from the cells of the cortical substance, which he calls "intercortical commissural fibres."[1] This view, however, is not adopted by the best anatomists; but nearly all agree that new fibres arise from the cells of the corpora dentata and contribute to the formation of the peduncles.

From the above sketch, the physiological significance of the direction of the fibres, as appears from the most reliable and generally-accepted anatomical investigations, is sufficiently evident. By the superior peduncles, the cerebellum is connected, as are all of the encephalic ganglia, with the cerebrum; by the middle peduncles, the two lateral halves of the cerebellum are intimately connected with each other; and by the inferior peduncles, the cerebellum is connected with the posterior columns of the spinal cord. We shall see, when we come to study the functions of the cerebellum, that its connection with the posterior white columns of the cord is a point of great interest and importance.

General Properties of the Cerebellum.—There is now no difference of opinion among physiologists, with regard to the general properties of the cerebellum. We may safely discard the observations of Zinn and Haller upon this point, for these experimenters, who conceived that irritation of the cerebellum produced convulsive movements,[2] undoubtedly stimulated portions of the medulla oblongata; at least, this must be assumed, if we accept the results of the more recent experiments of Flourens, Longet, and many others. Flourens, who made the first elaborate and entirely satisfactory observations upon the cerebellum in living animals, noted,

[1] LUYS, *Recherches sur le système nerveux cérébro-spinal*, Paris, 1865, p. 126, *et seq.*

[2] HALLER, *Mémoires sur la nature sensible et irritable des parties du corps animal*, Lausanne, 1756, p. 208.

in all of his experiments, that lesion or irritation of the cerebellum alone produced neither pain nor convulsions;[1] and the same results have followed the observations of Longet[2] and of all modern physiologists who have investigated this question practically. We have ourselves frequently exposed and mutilated the cerebellum in pigeons, and have never observed any evidence of excitability or sensibility. From these facts, we must conclude that the cerebellum is inexcitable and insensible to direct stimulation, at least as far as has been shown by direct observations. It is not impossible, however, that future experiments may reverse this generally-received opinion; particularly in view of the recent observations of Fritsch and Hitzig, already cited,[3] which show that certain parts of the cerebrum are excitable, and that the excitability of the encephalic centres rapidly disappears in living animals, as the result of pain and hæmorrhage. We should note, also, the experiments of Budge, who observed movements in the testicles and vasa deferentia, in males, and in the cornua of the uterus and the Fallopian tubes, in females, following irritation of the cerebellum.[4] Hammond noted movements of this kind in cats just killed, and also movements of the intestines and of the muscles of the abdomen, thigh, and back.[5]

Functions of the Cerebellum.

There are still the widest differences of opinion among physiologists, with regard to the functions of the cerebellum, mainly for the reason that the experiments upon the lower

[1] FLOURENS, *Recherches expérimentales sur les propriétés et les fonctions du système nerveux*, Paris, 1842, p. 18.

[2] LONGET, *Anatomie et physiologie du système nerveux*, Paris, 1842, tome i., pp. 733, 734.

[3] See page 323.

[4] BUDGE, *Lehrbuch der speciellen Physiologie des Menschen*, Leipzig, 1862, S. 788.

[5] HAMMOND, *Physiology and Pathology of the Cerebellum.—Quarterly Journal of Psychological Medicine*, New York, 1869, vol. iii., p. 223.

animals, made by Flourens and his followers, though in themselves sufficiently definite, are apparently contradicted by pathological observations upon the human subject. There should be no such discrepancy between well-conducted experiments and carefully-observed cases of disease or injury; for it is certain that the functions of the cerebellum present no essential differences in different animals, at least in man, the mammalia, and birds. It is necessary, therefore, for the physiologist, by carefully analyzing and correcting the results obtained by direct experimentation, and by applying to the study of palological observations the facts elicited by these experiments, to endeavor to harmonize the real or apparent contradictions; for, as we have often had occasion to remark, there are no exceptions to the laws to which the functions of similar classes of animals are subordinated; and observations and experiments, apparently discordant, will always be found, as our positive knowledge advances, to present differences in the conditions under which the phenomena have been observed. To apply this to the functions of the cerebellum, it may be safely assumed that it is impossible for this organ to preside directly and exclusively over the muscular coördination in birds and the inferior mammals, and in man, to possess different functions. With regard to the cerebrum, man possesses, not only a higher degree of development of certain intellectual faculties than the inferior animals, but is endowed with others, such as the power of articulate language. But in man and in the higher orders of animals, the general properties and functions of the muscular system are essentially the same. To take one of the most generally-accepted views of the functions of the cerebellum, if this be the centre for muscular coördination in birds and mammals, it has the same office in man, though it may possess additional functions not found lower in the scale of animal life. Keeping in view, then, the desirability of bringing into accord the results of experiments and of pathological observations, we will first study carefully the

phenomena which follow injury or extirpation of the cerebellum in animals.

Extirpation of the Cerebellum in Animals.—In birds, and in certain mammals in which the operation has been successful, the more or less complete extirpation of the cerebellum is followed by well-marked phenomena, presenting always the same character, but somewhat differently interpreted by various experimenters. Experiments of this kind were first made by Flourens; and the accuracy of his observations has never been successfully controverted, whatever may have been said of his physiological deductions. Indeed, there are few if any important points in the phenomena following partial or complete removal of the cerebellum that escaped the attention of this most accurate observer.

Laying aside, for the present, the deductions to be made from experiments on animals, the phenomena noted by Flourens and by all who have repeated his observations on the cerebellum are as follows:

"I extirpated the cerebellum by successive layers in a pigeon. During the removal of the first layers, there only appeared slight feebleness and want of harmony in the movements.

"At the middle layers, there was manifested an almost universal agitation, although there was not added any sign of convulsion; the animal executed sudden and disordered movements; it heard and saw.

"On the removal of the last layers, the animal, the faculty of jumping, flying, walking, and maintaining the erect position being more and more disturbed by the preceding mutilations, lost this faculty entirely.

"Placed on the back, it was not able to recover itself. Far from resting calm and steady, as occurs in pigeons deprived of the cerebral lobes, it became vainly and continually agitated, but it never moved in a firm and definite manner.

"For example, it saw a blow with which it was threatened,

wished to avoid it, made a thousand efforts to avoid it, but did not succeed. If it were placed on its back, it would not rest, exhausted itself in vain efforts to get up, and finished by remaining in that position in spite of itself.

"Finally, volition, sensation, perception, persisted; the possibility of making *general movements* persisted also; but the *coördination of the movements* in regular and definite acts of locomotion was lost."[1]

These are the phenomena observed after total extirpation of the cerebellum. Voluntary movement, sensation, general sensibility, and the special senses, seem to be intact; but there is always a loss of the power of equilibrium, and the movements executed are never regular, efficient and coördinate. Flourens farther states that animals operated upon in this way retain the intellectual and perceptive faculties.[2]

It is exceedingly important now to note the effects of partial removal of the cerebellum, as these bear directly upon cases of disease or injury of this organ in the human subject, in which its disorganization is very rarely complete. We may illustrate this also by citing two of Flourens's typical experiments:

"I. I removed by successive layers, all of the upper half of the cerebellum in a young cock.

"The animal immediately lost all stability, all regularity in its movements; and its tottering and *bizarre* mode of progression reminded one entirely of the gait in alcoholic intoxication.

"Four days after, the equilibrium was less disturbed, and the progression was more firm and assured.

"Fifteen days after, the equilibrium was completely restored.

"II. I removed, in a pigeon, about the half of the cerebellum; and I removed this organ completely in a fowl.

[1] FLOURENS, *Recherches expérimentales sur les propriétés et les fonctions du système nerveux*, Paris, 1842, p. 37.

[2] *Op. cit.*, p. 134.

"At the end of a certain time, the pigeon had regained its equilibrium; the fowl did not regain it at all: the latter lived nevertheless for more than four months after the operation."[1]

These important observations we have repeatedly confirmed, and have in our possession the encephalon of a pigeon which recovered completely after removal of about two-thirds of the cerebellum, the animal first presenting marked deficiency in coördinating power.

Such are the phenomena observed in experiments upon the cerebellum in birds, and they have been extended by Flourens[2] and others[3] to certain mammals, as young cats, dogs, moles, mice, etc. Our own experiments, which have been very numerous during the last twelve years, are simply repetitions of those of Flourens, and the results have been the same without exception.

The only difficulties in operating upon the cerebellum arise from hæmorrhage and the danger of injuring the medulla oblongata. The skull is exposed by slitting up the scalp, and the calvarium is removed in its posterior portion, penetrating just above the upper insertion of the cervical muscles. It is well to leave a strip of bone in the median line, thereby avoiding hæmorrhage from the great venous sinus, though this is not essential. The cerebellum is thus exposed, and may be removed in part or entirely, by a delicate scalpel or forceps, when the characteristic phenomena just described are observed. Animals operated upon in this way feel the sense of hunger and attempt to eat, but when the movements are very irregular, they are unable to take food. We have frequently compared the phenomena presented after removal of the cerebellum with the movements of a pigeon intoxicated by forcing down the œsophagus a

[1] FLOURENS, *op. cit.*, p. 102.

[2] *Op. cit.*, p. 138, *et seq.*

[3] VULPIAN, *Leçons sur la physiologie générale et comparée du système nerveux*, Paris, 1866, p. 606.

little bread impregnated with alcohol, and they present a striking similarity.

In view of the remarkable uniformity in the actual results obtained by different experimenters, it is hardly necessary to cite all of the observations made upon the lower animals. The phenomena observed by Flourens have been in the main confirmed by Fodéra,[1] Bouillaud,[2] Magendie,[3] Wagner,[4] Lussana,[5] Hammond,[6] Dalton,[7] Vulpian,[8] Mitchell,[9] Onimus,[10] and many others. Certain of these authors differ from Flourens in their ideas concerning the functions of the cerebellum, while they admit the accuracy of his observations.

We will eliminate from the present discussion the experiments made upon animals low in the scale, such as frogs and fishes, though in some of these, the results are in accord with the observations just cited upon birds and mammals,[11] and confine ourselves to an interpretation of the phenomena observed after extirpation of the cerebellum in animals in which the muscular and nervous arrangement is like that of the

[1] FODÉRA, *Recherches expérimentales sur le système nerveux.—Journal de physiologie*, Paris, 1823, tome iii., p. 193.

[2] BOUILLAUD, *Recherches expérimentales tendant à prouver que le cervelet préside aux actes de la station et de la progression.—Archives générales de médecine*, Paris, 1827, tome xv., p. 68, *et seq.*

[3] MAGENDIE, *Précis élémentaire de physiologie*, Paris, 1836, tome i., p. 409.

[4] WAGNER, *Recherches critiques et expérimentales sur les fonctions du cerveau.—Journal de la physiologie*, Paris, 1861, tome iv., p. 258.

[5] LUSSANA, *Leçons sur les fonctions du cervelet.—Journal de la physiologie*, Paris, 1862, tome v., p. 418.

[6] HAMMOND, *The Physiology and Pathology of the Cerebellum.—Quarterly Journal of Psychological Medicine*, New York, 1869, vol. iii., p. 230.

[7] DALTON, *Human Physiology*, Philadelphia, 1871, p. 445.

[8] VULPIAN, *Système nerveux*, Paris, 1866, p. 618.

[9] S. WEIR MITCHELL, *Researches on the Physiology of the Cerebellum.—American Journal of the Medical Sciences*, Philadelphia, 1869, New Series, No. cxiv., p. 331.

[10] ONIMUS, *Recherches expérimentales, etc.—Journal de l'anatomie*, Paris, 1870-1871, tome vii., p. 652, *et seq.* Onimus believes that the cerebellum presides over equilibration rather than general muscular coördination.

[11] VULPIAN, *op. cit.*, p. 689.

human subject. The results of this mutilation are as definite, distinct, and invariable, as in any experiments on living animals, and, taken by themselves, lead inevitably to but one conclusion.

When the greatest part or the whole of the cerebellum is removed from a bird or mammal, the animal being, before the operation, in a perfectly normal condition, and no other parts being injured, there are no phenomena constantly and invariably observed except certain modifications of the voluntary movements. The intelligence, general and special sensibility, the involuntary movements, and the simple faculty of voluntary motion, remain. The movements are always exceedingly irregular and incoördinate; the animal cannot maintain its equilibrium; and, on account of the impossibility of making regular movements, it cannot feed. This want of equilibrium and of the power of coördinating the muscles of the general voluntary system causes the animal to assume the most absurd and remarkable postures, which, to one accustomed to these experiments, are entirely characteristic. Call this want of equilibration, of coördination, of "muscular sense," an indication of vertigo, or what we will, the fact remains, that regular and coördinate muscular action in standing, walking, or flying, is impossible, although voluntary power remain. It is well known that many muscular acts are more or less automatic, as in standing, and, to a certain extent, in walking. These acts, as well as nearly all voluntary movements, require a certain coördination of the muscles, and this, and this alone, is abolished by extirpation of the cerebellum. It is true that destruction of the spiral canals of the internal ear produces analogous disorders of movement,[1] but this is the only mutilation, except division

[1] FLOURENS, *Recherches expérimentales sur les propriétés et les fonctions du système nerveux*, Paris, 1842, p. 446.

GOLTZ, *Ueber die physiologische Bedeutung der Bogengänge des Ohrlabyrinths.—Archiv für die gesammte Physiologie*, Bonn, 1870, Bd. iii., S. 172, *et seq.*

Taking the results of his experiments as a basis, Goltz proposes the theory that the semicircular canals are the organs presiding over the sense of equilib-

of the anterior white columns of the cord, which produces any thing like the results of cerebellar injury. Certain important coördinate muscular movements are well known to be dependent upon distinct nerve-centres. The acts of respiration are presided over exclusively by the medulla oblongata. Deglutition probably has its distinct nerve-centre, as well as the movements of the eyes. The centre regulating the coördinate movements in speech is situated in the anterior cerebral lobes. None of these peculiar movements are affected by extirpation of the cerebellum.

If there be a distinct nerve-centre which presides over the coördination of the general voluntary movements, experiments upon the higher classes of animals show that this centre is located in the cerebellum. It may be either in the entire cerebellum or in a certain portion of this organ, but if it be confined to a restricted part, this has not yet been determined. If the cerebellum preside over coördination, as a physiological necessity, the centre must be connected by nerves with the general muscular system. If this connection exist, a complete interruption of the avenue of communication between the cerebellum and the muscles, we would naturally expect, would be followed by loss of coördinating power. From the anatomical connections of the cerebellum, it appears that the only communication between this organ and the general system is through the posterior white columns of the spinal cord. We have seen that these columns are not for the transmission of the general sensory impressions, and there is no satisfactory evidence that they convey to the encephalon the so-called muscular sense. As regards general sensibility and voluntary motion, we cannot ascribe any function to the posterior

rium of the head, and thereby of the whole body; that the pressure of the liquid in these canals varies with the movements of the head, and that the brain receives from these, information with regard to the position of the head, and is able to regulate the general movements accordingly; and that this information is inaccurate when the pressure of liquid in the canals is abnormal, the result being disturbance of the general equilibrium.

white columns, except that when they are divided at several points, we invariably have want of coördination in the general muscular system.[1] When the posterior white columns are disorganized in the human subject, we have loss or impairment of coördinating power, even though the general sensibility be not affected, as in the disease called locomotor ataxia.

Confining ourselves still to the interpretation of experiments upon living animals, and leaving for subsequent consideration the phenomena observed in cases of disease or injury of the cerebellum in the human subject, we are led to the following conclusions:

There is a necessity for coördination of the movements of the general voluntary system of muscles, by means of a nerve-centre or centres.

Whatever other functions the cerebellum may have, it acts as the centre presiding over equilibration and general muscular coördination.

The cerebellum has its nervous connection with the general muscular system through the posterior white columns of the spinal cord, a fact which is capable both of anatomical and physiological demonstration.

If the cerebellum be extirpated, there is loss of coördinating power; and if the posterior white columns of the cord be completely divided, destroying the communication between the cerebellum and the general system, there is also loss of coördinating power.

When a small portion only of the cerebellum is removed, there is slight disturbance of coördination, and the disordered movements are marked in proportion to the extent of injury to the cerebellum.

After extirpation of even one-half or two-thirds of the cerebellum, the disturbances in coördination immediately

[1] The reader is advised to study, in this connection, that portion of the chapter on the spinal cord as a conductor, which treats of the probable functions of the posterior white columns (see page 289).

following the operation may disappear, and the animal may entirely recover, without any regeneration of the extirpated nerve-substance. This important fact enables us to understand how, in certain cases of disease of the cerebellum in the human subject, when the disorganization of the nerve-tissue is slow and gradual, there may never be any disorder in the movements.

We present the above conclusions, as in our own mind positive and definite. It is proper to state, however, that the definition of the function of the cerebellum is one of the points stated by most physiological authors as doubtful and unsettled; and this is so, mainly because many writers have been unable to harmonize the experimental facts above detailed, with cases of disease or injury of the cerebellum in the human subject. We conceive that this has frequently been due to an imperfect study of the pathological facts, which we now propose to investigate as thoroughly as possible.

Pathological Facts bearing upon the Functions of the Cerebellum.—Nearly all writers on the physiology of the nervous system, while they agree that extirpation of the cerebellum in the lower animals produces irregularity of movements, are arrested, as it were, in their deductions, by the following quotation from Andral, in his report of ninety-three cases of disease of the cerebellum:

"A more remarkable alteration of movement is noted in the observation of M. Lallemand. The patient staggered on his legs, and often came near falling forward. In this case, the only one which tends to confirm the opinion of physiologists who regard the cerebellum as the organ of the coördination of movements, the cerebellum was entirely transformed into a sac filled with pus." [1]

[1] Andral, *Clinique médicale*, Bruxelles, 1834, tome v., p. 501.

The case alluded to is quoted from Lallemand, which we have consulted in the original, and will refer to again.

The bare statement, such as is generally made, that Andral collected ninety-three cases of disease of the cerebellum, only one of which tends to show that this is the organ of muscular coördination, is sufficient to arrest any physiologist in the conclusions that would naturally be drawn from experimental facts; and nearly all writers have expressed themselves as uncertain upon the question of the function of the cerebellum. Before we go any farther, we wish to settle, once for all, the physiological bearing of these cases; and, with this end in view, have carefully studied, analyzed, and tabulated them. Out of the ninety-three cases, fifteen were observed by Andral, and seventy-eight are quoted from various authors. An analysis of these cases, with reference to conditions likely to complicate the effects of the cerebellar disease, etc., is given in the following table:

Analysis of Andral's ninety-three Cases of Disease of the Cerebellum.

(*Six Cases, observed by Andral.*)

Hemiplegia; death in fifty hours	1 case.
Hemiplegia; sudden death	1 "
Hemiplegia; death in two days	1 "
Hemiplegia; associated with cerebral hæmorrhage	3—6[1] cases.

(*Seventy-eight Cases, quoted from various Authors.*)

Hæmorrhage into the cerebellum;			quoted from Serres	6 * cases.
"	"	"	quoted from Dance	1 † case.
"	"	"	quoted from Bayle	1 ‡ "
"	"	"	quoted from Guiot	1 § "
"	"	"	(Serres) hemiplegia	2 cases.
"	"	"	(Cazes) coma	1 case.
"	"	"	(Morgagni); found dead	1 "
"	"	"	(Sédillot); died in fifteen minutes	1 "
"	"	"	(Cafford); died suddenly	1 "
Hæmorrhage (Michelet); apoplexy two years before death; found an old clot in the right lobe of the cerebellum				1 "
				—16 cases.

[1] In these six cases, there was hæmorrhage into the cerebellum.

Brought forward	16	cases
Hæmorrhage (quoted from various authors); hæmorrhage into the cerebrum as well as the cerebellum	9	"
Atrophy of the left cerebral and the right cerebellar hemisphere	2	"
Cases of disease, with paralysis; quoted from various authors	9	"
Cases of abscess, with paralysis; quoted from various authors	3	"
Cyst (Récamier); convulsions	1	case.
Abscess (Laugier); convulsions	1	"
Abscess, involving the entire cerebellum (Lallemand); want of coördination[1]	1	"
Cases, quoted from various authors, in which no disturbance was noted in the movements; the disease was confined to one lateral lobe of the cerebellum	5	cases.
Cases of tumor, quoted from various authors, in which there was paralysis	15	"
Cases of tumor, associated with disease of the cerebrum	7	"
Cases of tumor, associated with convulsions; the descriptions are very indefinite	9—78	cases.

(*Nine Cases, observed by Andral.*)

Softening; hemiplegia and convulsions	1	case.
Softening; hemiplegia and subsequent hæmorrhage	1	"
Softening; hemiplegia and hæmorrhage	1	"
Softening; agitation, like convulsions, of the members	1	"
Cyst; paralysis and convulsions	1	"
Tubercle; hemiplegia	1	"
Five small tubercles in one hemisphere of the cerebellum; movements normal	1	"
Tuberculous mass, the size of a hazel-nut, on one side of the cerebellum; movements normal	1	"
Cyst, the size of a hazel-nut, on one side of the cerebellum; movements normal	1—9	cases.
Add cases of hæmorrhage, previously cited, observed by Andral,	6	"
Add cases quoted from various authors	78	"
Total cases collected by Andral[2]	93	cases.

In six cases, quoted from Serres, marked *, "there were observed all the signs of violent apoplexy; nothing in particular is said with regard to disorders of movement" (Andral, *op. cit.*, p. 475). In the case quoted from Dance,

[1] This is the single case, noted by Andral, out of the ninety-three, showing want of coördination.

[2] Andral, *Clinique médicale*, Bruxelles, 1834, tome v., p. 468, *et seq.*

marked †, the patient was struck with apoplexy (Andral, *op. cit.*, p. 475). In the case quoted from Bayle, marked ‡, the patient suddenly lost consciousness, had convulsive movements on the third day, and died in coma, on the fifth day (Andral, *op. cit.*, p. 476). In the case quoted from Guiot, marked §, there was "no lesion except effusion of blood in the median lobe of the cerebellum. The individual who was the subject of this observation had had an attack of apoplexy. Before his attack, he had for some time a tottering gait (*démarche chancelante*), and, after the attack, remained hemiplegic on the right side" (Andral, *op. cit.*, p. 476).

Let us now carefully review these ninety-three cases of Andral, which have been held *in terrorem* over those who have ventured to argue, from experiments on animals, that the cerebellum is the coördinator of the muscular movements, and see how many may properly be thrown out of the question!

We can discard the first six cases, observed by Andral, in which there was hemiplegia, speedy death, and in three of which, there was cerebral hæmorrhage; for we could hardly observe want of coördination in hemiplegics or in cases complicated with cerebral disease. We can discard the six cases, quoted from Serres, in which there was violent apoplexy, as well as the case quoted from Dance, with apoplexy and the case quoted from Bayle, with coma and convulsions. It is evident that these cases are useless in noting the presence or absence of coördinating power. We can discard two cases (Serres) with hemiplegia; one (Cazes) with coma; one, (Morgagni) found dead; one (Sédillot) died in fifteen minutes; one (Cafford) died suddenly; one (Michelet) apoplexy two years before death, and an old clot in the right lobe of the cerebellum. This last case is in accord with experiments on animals; for we have seen that the coördinating power may be restored after loss of one-half of the cerebellum. We can discard nine cases quoted from various authors, in which there was cerebral as well as cerebellar hæmor-

rhage; two cases of paralysis, with atrophy of one hemi sphere of the cerebrum and one hemisphere of the cerebellum; nine indefinitely described cases, with paralysis; three cases of abscess, with paralysis; one case of cyst and one of abscess, with paralysis; fifteen cases of tumor, with paralysis; seven cases, associated with disease of the cerebrum and paralysis; nine very indefinitely described cases, associated with convulsions. Of the remaining cases observed by Andral, we can discard one, with hemiplegia and convulsions; one, with hemiplegia and subsequent hæmorrhage; one, with hemiplegia; one case of cyst, with paralysis and convulsions; one, of tubercle, with hemiplegia. We can also discard one case of five small tubercles in one hemisphere of the cerebellum; one, of a tuberculous mass, the size of a hazel-nut, on one side; one, of a cyst, the size of a hazel-nut, on one side. These last cases do not present sufficient destruction of the cerebellar substance to lead us to expect any disorder in the movements.

Thus far we have discarded eighty-five cases, leaving eight to be analyzed. Of these eight cases, in five, it is simply stated that the movements were unaffected, and that "one of the lateral lobes of the cerebellum was the seat of abscess" (Andral, *op. cit.*, p. 500). In view of this bare statement, and the fact that, in animals, recovery of coördinating power takes place when half of the cerebellum has been removed, we may throw out these cases as incomplete. It must be remembered that the abscesses were probably of slow development; and if they did not destroy a sufficiently large portion of the cerebellum to influence the coördinating power permanently, it is not probable that the functions of this organ would be at all affected, as there would be no shock, as in the sudden removal of substance by an operation.

We are thus reduced to three cases; and in all of these, the movements were more or less affected. These cases we will now study as closely as is possible from the details given.

Case I.—The first case is quoted from Guiot. There was

no lesion, except an effusion of blood in the median lobe of the cerebellum, and there was probably no pressure upon the peduncles. "The individual who was the subject of this observation had had an attack of apoplexy. Before the attack, he had for some time a staggering gait (*une démarche chancelante*), and, after the attack, he had remained hemiplegic on the left side" (Andral, *op. cit.*, p. 476). From these meagre details, it seems probable that there was a certain amount of difficulty of coördination, though the description is not as definite as could be desired.

Case II.—The second case was observed by Andral. A groom, not quite forty years of age, was brought into the *Maison royale de santé*, having suffered from severe headache, vertigo, etc., for fifteen days, which finally became fixed at the occiput. During the first three days in the hospital, "he was in a continual state of agitation; the movements of the members, on the right as well as the left side, were sometimes so *brusques* and disordered that they resembled convulsive movements." Soon the respiration became disturbed, and he died in asphyxia. "Upon post-mortem examination, there was found general injection of the meninges; nothing particular in the cerebral hemispheres; a moderate quantity of serum in the ventricles; reddish softening of the left hemisphere of the cerebellum in its posterior and inferior half; no other lesion" (Andral, *op. cit.*, p. 490).

The only marked symptom relating to the movements in this case was a certain amount of irregularity and convulsive action of the muscles, while the patient was in bed. The case is not strong in its bearings, either for or against the coördination-theory; for there must have been a great amount of irritation of the encephalic centres, and it would certainly be difficult to note disturbance of equilibration or of coördination in a patient confined to the bed.

The third case is quoted by Andral from Lallemand, and is taken by Lallemand from Delamare.

Case III.—"M. Guérin, vicar at Gézeville, forty-six years of age, of a good temperament, strong, and corpulent, with a good appetite, complained of a dull pain, which finally became acute, under the frontal bone. For a year he experienced attacks of vertigo and vomiting, without fever. He staggered on his legs, and was often near falling forward. The treatment employed was antiphlogistic and derivative."

On post-mortem examination, the cerebrum was found entirely healthy, but the envelop of the cerebellum was collapsed, folded, and only contained about the half of an egg-shell full of a brown and fetid, lymphatico-purulent liquid.[1]

This case, as far as the description goes, shows marked difficulty in equilibration or coördination.

If the reader have carefully studied the foregoing analysis of Andral's cases, he will see that eighty-five may be thrown out altogether, leaving but eight; and of these eight cases, five are so imperfectly described, and the disorganization of the cerebellum is so restricted, that they may also be disregarded. The ninety-three cases are thus reduced to three. Of these three cases, in two, it is uncertain whether or not there were deficiency of coördinating power; and in one, the difficulty in equilibration or coördination was distinctly noted. This, we conceive, disposes of the much-quoted ninety-three cases of Andral; and they are certainly not opposed to the view that the cerebellum is the organ of equilibration or muscular coördination.

In addition to the cases collected by Andral, there are numerous other instances on record of disease confined to the cerebellum.

Case IV.—An interesting case of disease of the cerebellum was reported by Gall, in 1823.[2] This patient "complained for several months of a very disagreeable sense of pressure at the nucha, and a tendency to fall forward as if

[1] Lallemand, *Recherches anatomico-pathologiques sur l'encéphale*, Paris, 1823, tome ii., p. 39.

[2] Gall, *Sur les fonctions du cerveau*, Paris, 1823, tome iii., p. 341.

he saw a precipice at his feet. Several physicians attributed these symptoms to hæmorrhoids; for myself, I concluded that there was an organic disease in the brain. Several months after, the patient died, and we found on the tentorium a fleshy mass two inches in diameter, which had compressed the cerebellum."

Case V.—In 1826, Petiet reported a case of disease, in which the cerebellum was entirely destroyed, its tissue being broken down into a sort of whitish *bouillie*.[1] The cerebrum was healthy. The observation was made in 1796. The patient, before death, was observed to present a remarkable tendency to walk backward. He rose from his seat with difficulty, and, once erect, the first movements of the feet were lateral, and he finally walked by moving the feet from before backward. His locomotion consisted simply in passing from his own to an adjoining bed in the ward, a distance of about six feet.

Case VI.—One of the most remarkable cases, and the one most frequently quoted by physiological writers, was reported by Combette, in 1831.[2] This patient, Alexandrine Labrosse, in her seventh year, was seen by M. Miquel. Since the age of five years only had she been able to sustain herself on her feet. M. Miquel was struck with her slight development and the feebleness of the extremities. At the age of nine and a half years, she was admitted into the *Orphelins.* "When spoken to, she answered with difficulty and hesitation. Her legs, although very feeble, enabled her still to walk, but she often fell." She was first seen by M. Combette, in January, 1831. She had then kept the bed for three months; was constantly lying on the back, and could scarcely move the legs; she used her hands with ease. She died of some intestinal disorder, March 25, 1831. On post-

[1] Petiet, *Journal de physiologie*, Paris, 1826, tome vi., p. 162, *et seq.*

[2] Combette, *Observation d'une jeune fille, morte dans sa onzième année, chez laquelle il y avait absence complète du cervelet, des pédoncules postérieures et de la protubérance annulaire.—Journal de physiologie*, Paris, 1831, tome xi., p. 27, *et seq.*

mortem examination, "in place of the cerebellum there was a cellular membrane, gelatiniform, semicircular, from eighteen to twenty lines in its transverse diameter." There was no trace of the pons Varolii. Combette states that Alexandrine Labrosse was able to walk for several years, always, it is true, in an uncertain manner; later, her legs became more and more feeble, and finally she ceased to be able to sustain her weight. She had the habit of masturbation. Combette further states that this observation is not in accord "with the experiments of Flourens, which tend to show that the cerebellum is the regulator of movements." The encephalon was also examined by Guillot, who noted absence of the cerebellum and of the pons.

This case is somewhat imperfect, as it was not seen by Combette until the patient had kept the bed for three months. By some writers, it is quoted in favor of, and by some, in opposition to the view that the cerebellum coördinates the muscular movements. It was not a case of simple disease of the cerebellum, as the pons and the posterior peduncles were also absent. It was noted, before the case was seen by Combette, that the patient walked in an uncertain manner and often fell.

Several cases of injury of the cerebellum are reported by Larrey.[1]

Case VII.—One case is described, in which the patient was struck by a ball from a blunderbuss, which grazed the occipital protuberances. There was no disturbance of movement. The patient died on the thirty-ninth day, in opisthotonos. On post-mortem examination, "the occipital bone had sustained a considerable loss of substance; the slit into the dura mater, to which we have alluded, corresponded to the centre of the right lobe of the cerebellum, which was sunk downward and was of a yellowish color, but free from suppuration or effusion. The medulla oblongata and spinal

[1] Larrey, *Injuries of the Cerebellum.—Observations on Wounds, etc.*, Philadelphia, 1832, p. 199, *et seq.*

marrow bore a dull, white aspect, were of greater consistence than is natural, and had lost about a quarter of their size; the nerves arising from them appeared to us also to be in a state of atrophy near their origin" (Larrey, *op. cit.*, p. 207).

CASE VIII.—Another patient was struck by a piece of wood on the right side of the head. He was found dead a little over three months after the injury. "The right hemisphere of the cerebellum was entirely disorganized by an abscess which pervaded its whole substance" (Larrey, *op. cit.*, p. 210). No disturbances of movement were noted.

CASE IX.—Another patient had erysipelas following a fall on the side of the head, and abscess. He lived for three or four months. Five or six weeks after the injury, he had severe pains in the occiput, and, "when standing he could with difficulty only preserve his equilibrium." On post-mortem examination, the deep-seated vessels of the cerebrum were found injected. "We found, in the left lobe of the cerebellum, about three tablespoonfuls of pus of a whitish and gelatinous aspect, which had encroached upon, or rather displaced entirely, the hemisphere of the cerebellum; this purulent substance was enveloped within the pia mater, which had acquired a somewhat firmer consistence, and, as in the subject of the preceding case, assumed a pearly color. The other half of the cerebellum was shrivelled, and the medullary substance forming the arbor vitæ was of a grayish color and very dense" (Larrey, *op. cit.*, p. 211).

The first of these cases was found by Larrey to be associated with extinction of sexual appetite, and atrophy of the organs of generation. In the first two cases, judging from the results of experiments on animals, there was not enough injury of the cerebellum to necessarily influence the power of coördination. In the last case, there was difficulty in equilibration, but also some paralysis.

A number of cases, which it is unnecessary to detail fully, are cited by Wagner, in the *Journal de la physiologie*,

in which tottering gait and want of equilibration or of muscular coördination were noted, in connection with greater or less disorganization of the cerebellum.[1] In the same journal, is a brief note of a case, reported by Laborde, in which there was a large cyst in the cerebellum, with incomplete paraplegia and "want of coördination of the movements of progression."[2]

CASE X.—A most remarkable and carefully-observed case of atrophy of the cerebellum was reported by Dr. Fiedler, in 1861.[3] The subject of this observation, a man, aged about fifty years, had remarkable peculiarities in his movements for thirty years. After the age of twenty years, it is stated that "he could no longer walk with as much certainty as before; the gait was staggering (*taumelnd*). . . . Not only in the house, but also in the street, the patient often fell, so that he was very frequently taken for a drunkard, and was either carried home or taken to the police-station. It is said that he never had drunk spirituous liquors.

"Sometimes the patient walked backward, but only a few steps. He never had any turning movements; the gait was always tottering (*wacklig*) and slow" (Fiedler, *op. cit.*, p. 251). He never fell forward, but always on the back. On post-mortem examination, the cerebrum was found healthy, "but the cerebellum was atrophied, especially at its posterior and inferior portion, and was reduced in size at least one-half" (Fiedler, *op. cit.*, p. 258). This case presented the phenomena of defective coördination to a marked degree. Nothing is said of vertigo.

CASE XI.—In an elaborate article by Lussana, on the cerebellum, a case is quoted from Pourfour du Petit, in which a soldier, who received a gunshot-wound traversing

[1] WAGNER, *Recherches critiques et expérimentales sur les fonctions du cerveau.—Journal de la physiologie*, Paris, 1861, tome iv., p. 386.

[2] Ibid., p. 637.

[3] FIEDLER, *Ein Fall von Verkümmerung des Cerebellum.—Zeitschrift für rationelle Medicin*, Leipzig und Heidelberg, 1861, Bd. xi., S. 250, *et seq.*

the left lobe of the cerebellum, immediately presented "a great disorder in his movements." [1]

Among the most striking of the cases of disease of the cerebellum, are two observed by Vulpian.

CASE XII.—The first was a woman, forty-nine years of age, in the hospital of *la Salpêtrière.* "All of the movements were preserved, but locomotion was most irregular and difficult; she could only walk in the most *bizarre* manner, resting on a chair which she placed before her at every step, and, in spite of her efforts at equilibration, she often fell." This patient, however, retained great muscular power. On post-mortem examination, "the cortical gray substance of the cerebellum was found entirely atrophied: all the nerve-cells of this layer had disappeared." There was considerable reduction in the size of the cerebellum. The corpora dentata were perfectly preserved, "showing that these parts, at all events, have but a slight office in coördination." [2]

CASE XIII.—The second case presented an old softening, about the size of a hazel-nut, destroying a corresponding amount of the cerebellar substance of one of the hemispheres. The corpus dentatum was completely destroyed. This woman "walked well, but it appears nevertheless that she vacillated very slightly in her gait, without, however, a tendency to fall." [3]

We have thus cited quite a number of cases of disease confined to the cerebellum, in which there was marked disturbance in the muscular movements; but there are others, in which the movements were unaffected. As an example of the latter, we may refer to a case cited from Bouvier, by Prof. Hammond.

CASE XIV.—In this case, the movements of the limbs were all preserved. On post-mortem examination, there was found an abscess involving the two outer thirds of the

[1] LUSSANA, *Leçons sur les fonctions du cervellet.—Journal de la physiologie,* Paris, 1862, tome v., p. 429.

[2] VULPIAN, *Système nerveux,* Paris, 1866, p. 629. [3] *Op. cit.,* p. 632.

left hemisphere of the cerebellum; the walls of this cavity, which contained several tablespoonfuls of pus, were softened.

"As M. Bouvier remarks, a circumstance of great interest connected with this case is the entire absence during life of any symptoms indicating an augmented sensibility, loss of equilibrium, or excitation of the genital organs."[1]

With regard to this case, it is evident that the disease of the cerebellum was of slow development and did not involve enough of its substance to necessarily interfere with its functions, as has been clearly shown in other pathological cases and in experiments upon animals.

Prof. Hammond also reports two interesting cases which came under his own observation.[2]

Case XV.—"In 1851, a Mexican shepherd was attacked near Cebolleta, in New Mexico, by Navajo Indians. He managed to escape, but in fleeing from his enemies received an arrow-wound in the posterior part of the head. He was on horseback, and, though stunned by the blow, maintained his seat in the saddle. So firmly was the arrow implanted that the shaft became detached by his efforts to remove it, leaving the head of the weapon in the skull. I saw him about two hours subsequently. He was then in full possession of his senses and was suffering no pain. There were, however, constant vertigo and nausea, together with a sensation, as he described it, as if his head were balanced on a very delicate point, and the least inclination to one side or the other would cause it to fall off. On examining the wound, I found the arrow still sticking in the bone, and I had to use considerable force before I could remove it. It had entered to the extent of an inch and a half—a little below and to the left of the occipital protuberance—wounding the left lobe of the cerebellum. The vertigo continued all

[1] Hammond, *The Physiology and Pathology of the Cerebellum.—Quarterly Journal of Psychological Medicine*, New York, 1869, vol. iii., p. 237.

[2] *Loc. cit.*

that night, but the nausea and vomiting stopped in the course of a few hours.

"The next day he attempted to walk, but was obliged to desist on account of the vertigo. 'He felt,' he said, 'as if he were drunk,' and he staggered just like a drunken man. This feeling of vertigo continued for several weeks, lasting all through the period of suppuration. Gradually it disappeared, though even after the lapse of a year he felt giddy on making any unusual exertion. At no time was there any difficulty in coördinating the muscles of the upper or lower extremities. The latter were simply affected through the vertigious sensation. The sensibility was unaffected throughout the whole progress of the case.

Case XVI.—"The other case was that of a man who, for several months, had suffered with vertigo, occasional convulsions, attacks of nausea and vomiting, and a constant and violent pain affecting the back of the head. These symptoms had come on subsequently to a severe blow which he had received on the back of the head, in consequence of raising himself too soon while the horse he was riding was passing under a low archway.

"When this man attempted to walk he reeled and staggered as if he were drunk, but his movements were very different from those which we now recognize as characterizing locomotor ataxia. The upper extremities, and the organs of speech, were not affected; he had the entire control of his legs when lying down, and there was no diminution of sensibility anywhere. At last he became paraplegic, and died in a convulsion. The *post-mortem* examination showed the existence of an abscess, which had obliterated nearly the whole of the left lobe of the cerebellum."

The interpretation of these two cases depends, apparently, upon the ideas concerning the functions of the cerebellum, with which they are regarded. We should consider them as very strong evidence that the cerebellum regulates equilibration and muscular coördination. Prof. Hammond re-

gards them as in accordance with his idea, that injury of the cerebellum does not affect coördination, but simply produces vertigo. It remains for the reader to judge whether or not the phenomena observed indicate want of coördinating power.

We now come to the main question, whether or not, in view of the results of experiments on animals and the phenomena observed in cases of disease or injury of the cerebellum, this nerve-centre presides over coördination of action of the muscles, which is certainly necessary to equilibration, except the muscles of the face and those concerned in speech. This question seems to us to be capable of a definite answer.

Every carefully-observed case that we have been able to find, in which there was uncomplicated disease or injury of the cerebellum, provided the disease or injury involved more than half of the organ, presented great disorder in the general movements, particularly those of progression. We have collected the more or less complete reports of sixteen cases. In Case II., there was softening of one-half of one hemisphere, and remarkable convulsive movements. In Case VI., the one so often quoted from Combette, the gait was uncertain, with frequent falling; there was incomplete paralysis; but, in addition to the absence of the cerebellum, there was no pons Varolii. In Case VII., there was no disturbance of movement, and there was partial degeneration of one lateral lobe. In Case VIII., there was no disturbance of movement, and disorganization of one lateral lobe of the cerebellum. In Case XIII., there was slight loss of substance in one lateral lobe of the cerebellum, and slight "vacillation" in the movements. In Case XIV., there was an abscess involving two-thirds of one lateral lobe, and the movements of the limbs were preserved. In Cases I., III., IV., V., IX., X., XI., XII., XV., XVI., ten out of sixteen, there was difficulty in muscular coördination, which was invariably in

direct ratio to the amount of cerebellar substance involved in the disease or injury. We do not make the reservation, that more than half of the cerebellum must be destroyed in order necessarily to produce difficulty in muscular coördination, on purely theoretical grounds, but regard this point as positively demonstrated by experiments on animals. These experiments show that one-half of the organ is capable of performing the function of the whole. We have an analogy to this in the action of the kidneys, one of which is sufficient for the elimination of the effete constituents of the urine, after the other has been removed.

Notwithstanding the contrary views of many physiological writers, we are firmly convinced, from experiments and a careful study of pathological facts, that there is no one point in the physiology of the nerve-centres more definitely settled than that the cerebellum presides over equilibration and the coördination of the muscular movements, particularly those of progression. In this statement, we make exceptions in favor of the movements of respiration, deglutition, of the face, and of those concerned in speech, as well as the involuntary movements generally. As another example of a nerve-centre presiding over muscular coördination, we have the instance of the portion of the left anterior lobe of the cerebrum, which coördinates the action of the muscles concerned in speech.

The theory that the disordered movements which follow injury of the cerebellum are due simply to vertigo is not tenable. In only three of the cases cited, is vertigo mentioned; and in two, the word vertigo seems to be used rather as an explanation of the phenomena observed, than in their simple description. There is a disease involving the semicircular canals and other parts of the internal ear, called Ménière's disease, in which there is marked want of equilibration and muscular coördination, attended with, and probably dependent upon vertigo. The vertigo is always very distinct, and is mentioned in all of these cases; and

though it is less in the recumbent posture, it is never entirely absent. A very elaborate article on certain affections of the inner ear, including Ménière's disease, with numerous illustrative cases, was published by Dr. Knapp, in the *Archives of Ophthalmology and Otology*, New York, 1871, vol. ii., No. i. A careful study of these cases, comparing them with the cases of deficient coördination from disease of the cerebellum, cannot fail to show a great difference between the phenomena following cerebellar disease and the muscular phenomena due to well-marked and persistent vertigo.[1]

Connection of the Cerebellum with the Generative Function.—The fact that the cerebellum is the centre for equilibration and the coördination of certain muscular movements does not necessarily imply that it has no other functions. The idea of Gall, that "the cerebellum is the organ of the instinct of generation,"[2] is sufficiently familiar; and there are numerous facts in pathology that show a certain relation between this nerve-centre and the organs of generation, though the idea that it presides over the generative function is not sustained by the results of experiments on animals, or by facts in comparative anatomy.

In experiments on animals in which the cerebellum has been removed, there is nothing pointing directly to this part as the organ of the generative instinct. Flourens removed a great part of the cerebellum in a cock. The animal survived for eight months. It was put several times with hens, and always attempted to mount them, but without success, from want of equilibrium. In this animal, the testicles were enormous.[3] This observation has been repeatedly confirmed, and there are no instances in which the cerebellum has been

[1] Knapp, *A Clinical Analysis of the Inflammatory Affections of the Inner Ear*, New York, 1871.

[2] Gall, *Sur les fonctions du cerveau*, Paris, 1825, tome iii., p. 245.

[3] Flourens, *Système nerveux*, Paris, 1842, p. 163

removed with apparent destruction of sexual instinct. In a comparison of the relative weights of the cerebellum in stallions, mares, and geldings, Leuret found that, far from being atrophied, the cerebellum of geldings was even larger than in either stallions or mares.[1]

In the numerous cases of disease or injury of the cerebellum, to which we have already referred, there are some, in which irritation of this part has been followed by persistent erection and manifest exaggeration of the sexual appetite, and others, in which its extensive degeneration or destruction has apparently produced atrophy of the generative organs and total loss of sexual desire. There are also certain cases of this kind which we have not yet cited. Serres gives the history of several cases, in which irritation of the cerebellum was followed by satyriasis or nymphomania, but in other cases, there were no symptoms referable to the generative organs.[2] In the case reported by Combette, the patient had the habit of masturbation.[3] Dr. Fisher, of Boston, gives an account of two cases of diseased or atrophied cerebellum, with absence of sexual desire, and one case of irritation, with satyriasis.[4] Similar instances are given by other writers, which it is unnecessary to detail. We have already cited the observations of Budge and of Hammond, in which mechanical irritation of the cerebellum was followed by movements of the uterus, testicles, etc.[5] For other citations bearing upon the connection between the cerebellum and the generative function, the reader is referred to the elaborate memoir by Prof. Hammond.[6]

[1] LEURET, *Anatomie comparée du système nerveux*, Paris, 1839–1857, tome i., p. 429.

[2] SERRES, *Sur les maladies organiques du cervelet.—Journal de physiologie*, Paris, 1822, tome ii., p. 172, *et seq.*, and p. 249, *et seq.*

[3] *Journal de physiologie*, Paris, 1831, tome xi., p. 30.

[4] FISHER, *Contributions Illustrative of the Functions of the Cerebellum.—American Journal of the Medical Sciences*, Philadelphia, 1838, No. xlv., p. 352, *et seq.*

[5] See page 363.

[6] *Quarterly Journal of Psychological Medicine*, New York, 1869, vol. iii., p. 219, *et seq.*

Although there are many facts in pathology which are opposed to the view that the cerebellum presides over the generative function, there are numerous cases which go to show a certain connection between this portion of the central nervous system and the organs of generation in the human subject. But this is all that we can say upon this important point; certain it is that the facts are not sufficiently numerous, definite, and invariable, to sustain the doctrine that the cerebellum is the seat of the sexual instinct.

Development of the Cerebellum in the Lower Animals.—The study of the comparative anatomy of the cerebellum has little physiological interest, except in so far as it bears upon our knowledge of its physiology. From this point of view, there is little to be said concerning its development in the animal scale. We can hardly establish a definite relation between this particular part of the encephalon and the complicated character of the muscular movements; for, as we pass from the lower to the higher orders of animals, we have other parts of the brain, as well as the cerebellum, developed in proportion to the increased complexity of the muscular system. Nor can we connect the comparative anatomy of the cerebellum with the ideas of the functions of this organ in connection with generation. The amphioxus lanciolatus has no cerebellum, and this organ, therefore, is not indispensable to generation. In some animals remarkable for salacity, the cerebellum is not unusually large; and facts of this kind might be multiplied *ad infinitum*.

Paralysis from Disease or Injury of the Cerebellum.—It is not unusual to observe disorganization of a considerable amount of cerebellar substance without paralysis; and, indeed, we are inclined, upon this point, to adopt the view advanced by Vulpian, that, of itself, disease of the cerebellum is not attended with hemiplegia, this condition obtaining only when the peduncles, the pons, or the motor tracts of

the cord are directly or indirectly involved.[1] As far as the physiology of the cerebellum bears upon this point, there is no reason why simple disease of its substance should produce hemiplegia. As in cerebral affections disease of the hemispheres is followed by hemiplegia, as the rule, only when the corpora striata, the optic thalami, or the pons, is involved, either by compression or disorganization, so in disease of the cerebellum, there must be some disturbance of the motor tracts.

It is a curious fact, also, that in certain cases of disease of the cerebellum, without any affection of the cerebrum, in which hemiplegia exists, the paralysis occurs on the opposite side of the body, while in others, it is on the same side as the cerebellar lesion. According to Vulpian, the hemiplegia is direct or crossed, the situation of the paralysis depending upon the parts of the motor tracts that are compressed. In simple softening of the substance of the cerebellum, as we have just remarked, there is, of necessity, no paralysis, but hæmorrhage or tumors may impinge upon one or another of the motor tracts of the encephalon or the cord.[2]

In certain of the cases collected by Andral, there was a lesion of one lateral lobe of the cerebellum, associated with a lesion of the cerebral hemisphere of the opposite side. In these cases, the paralysis did not affect both sides of the body, but was always situated on the side opposite to the lesion of the cerebrum, the same side as the cerebellar disease.[3]

We have thus only discussed those views with regard to the functions of the cerebellum which are supported by experimental or pathological facts, and have not touched upon the vague and unsupported ideas advanced by various writers before the publication of the remarkable observations of Flourens. There is no proof that the cerebellum is the organ

[1] VULPIAN, *Système nerveux*, Paris, 1866, p. 608.

[2] VULPIAN, *loc. cit.*

[3] ANDRAL, *Clinique médicale*, Bruxelles, 1834, tome v., p. 481.

presiding over memory, the involuntary movements, general sensibility, or the general voluntary movements. The only view that has any positive experimental or pathological basis is that it presides over equilibration and the coördination of certain muscular movements, and is in some way connected with the generative function.

CHAPTER XIV.

GANGLIA AT THE BASE OF THE ENCEPHALON.

Corpora striata—Optic thalami—Tubercula quadrigemina, or optic lobes—Ganglion of the tuber annulare—Medulla oblongata—Physiological anatomy of the medulla oblongata—Functions of the medulla oblongata—Connection of the medulla oblongata with respiration—Vital point—Connection of the medulla oblongata with various reflex acts—Rolling and turning movements following injury of certain parts of the encephalon—General properties of the peduncles.

At the base of the encephalon, are found several collections of gray matter, or ganglia, some of which have functions distinct from those already described in connection with the cerebrum and the cerebellum; but most of them are so difficult of access in living animals, that we possess very little definite information, even with regard to their general properties. We have, however, a tolerably complete knowledge of the functions of the medulla oblongata and the tubercula quadrigemina, and have some idea of the physiology of the tuber annulare; but the functions of the corpora striata, optic thalami, ventricles, pineal gland, peduncles, etc., are not at all understood, and the speculations of the older writers, with the indefinite experiments of modern physiologists, upon these parts, will be passed over very briefly.

Corpora Striata.

These bodies are somewhat pear-shaped, and are situated at the base of the brain, partly without the cerebral hemispheres and partly embedded in their white substance.

Their rounded base is directed forward, and the narrower end, backward and outward. Their external surface is gray, and they present, on section, alternate striæ of white and gray matter, which appearance has given them the name of corpora striata. Between the narrow extremities of these bodies, are situated the optic thalami.

There is very little to be said with regard to the functions of the corpora striata. Longet has found them completely inexcitable and insensible to mechanical irritation.[1] The idea of Magendie, that a tendency to backward movements resided in these bodies, while the cerebellum exerted an antagonistic action, is not sustained by experiments.[2] When they are removed, disturbing the hemispheres as little as possible, there appears to be no paralysis, either of motion or sensation.[3]

We have obtained a little more information regarding the functions of the corpora striata, from cases of cerebral hæmorrhage in the human subject, than from experimental investigations. In apoplexy, when the corpus striatum on one side is alone involved, there is paralysis of motion of the opposite lateral half of the body, the general sensibility usually being unaffected. Facts of this kind show that the action of the corpora striata is crossed; and they further illustrate their connection with the motor tract from the hemispheres.

There is no reason to suppose that the corpora striata are the centres of olfaction, as was at one time thought, for they are sometimes absent in animals possessing very large olfactory nerves, and are very largely developed in the cetacea, in which the olfactory apparatus is rudimentary.[4]

Optic Thalami.

From their name, we should infer that the optic thalami have some important function in connection with vision;

[1] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 419.

[2] MAGENDIE, *Précis élémentaire de physiologie*, Paris, 1836, tome i., p. 404.

[3] LONGET, *loc. cit.*

[4] LONGET, *loc. cit.*

but they serve merely as beds for the optic commissures, and give to the nerves but very few fibres. They are oblong bodies, situated between the posterior extremities of the corpora striata, and resting upon the crura cerebri on the two sides. They are white externally, and, in their interior, present a mixture of white and gray matter. Longet has destroyed them upon the two sides, carefully avoiding injury of the optic tracts, and noted no interference with vision or the movements of the iris.

The optic thalami seem, from experiments upon animals, to have a peculiar crossed action upon the muscular system. While their mechanical irritation produces neither pain nor convulsive movements, showing that they are insensible and inexcitable, the extirpation of one optic thalamus produces enfeeblement of the muscles of the opposite lateral half of the body, without actual paralysis.[1] When both have been removed, there is general debility of the muscular system. It is unnecessary to refer to other experiments upon these parts, which have been very indefinite in their results, or to allude to the "circular" movements produced by lesion upon one side, involving also the crus cerebri; for, beyond the statement just made, the function of the optic thalami is unknown.

We derive but little information concerning the optic thalami from cases of cerebral hæmorrhage in the human subject; for it is not common to have disease involving these parts and not affecting other centres. In some cases of lesion limited to the optic thalamus on one side, there is paralysis of sensation of the opposite lateral half of the body, without actual paralysis of motion, though the movements are generally feeble. When the brain-lesion involves both the corpus striatum and the optic thalamus on one side, which is more common, there is paralysis of motion, with loss or disorder of sensibility, on the opposite side of the body. These facts illustrate, to a certain extent, the ana-

[1] Longet, *Traité de physiologie*, Paris, 1869, tome iii., pp. 412, 413.

tomical connection of the optic thalami with the sensory tracts, though, in experiments on animals, destruction of these parts does not necessarily affect the general sensibility.

Tubercula Quadrigemina.

These little bodies, sometimes called the optic lobes, are rounded eminences, two upon either side, situated just behind the third ventricle. The anterior, called the nates, are the larger. These are oblong and of a grayish color externally. The posterior, called the testes, are situated just behind the anterior. They are rounded, and rather lighter in color than the anterior. Both contain gray nervous matter in their interior. They are the main points of origin of the optic nerves, and are connected by commissural fibres with the optic thalami. In birds, the tubercles are two in number, instead of four, and are called the tubercula bigemina.

It is probable that the tubercula quadrigemina are inexcitable and insensible. When pain and convulsive movements have apparently followed their mechanical irritation in living animals, these phenomena have probably been due to excitation or stimulation of the motor or sensory commissural fibres which pass beneath them. At least, this seems to be the proper conclusion to draw from the experiments of Longet.[1]

As regards the function of the optic lobes, aside from their action as reflex nervous centres for the movements of the iris, there is little to be said, except that they preside over the sense of sight. They are easily reached and operated upon in birds, where they are very large, and, as Flourens demonstrated many years ago, their extirpation is followed by total loss of sight, as well as abolition of the reflex movements of the iris.[2] In birds and in those mammals in which

[1] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 407.

[2] FLOURENS, *Système nerveux*, Paris, 1842, p. 145.

they have been operated upon, the action in vision is crossed; *i. e.*, when the lobe is removed upon one side, the sight is lost in the opposite eye, vision in the eye upon the same side being unimpaired. We have long been in the habit, in class-demonstrations, of removing the optic lobe on one side from a pigeon, with the result just mentioned. The operation is quite simple: A part of the skull is removed by the side of one hemisphere, and the optic lobe is seen, in the form of a large, white tubercle, between the posterior portion of the cerebrum and the cerebellum. A little slit is then made in its capsule, and the interior is broken up carefully with a delicate forceps. The animal generally recovers from the operation, blinded in the eye upon the opposite side. In removing the portion of the skull, it is well not to go too far back, when there is danger of wounding the great venous sinus and complicating the operation by hæmorrhage.

In treating of the special sense of sight, in the next and last volume, we shall see that the decussation of the optic nerves is more complex in man than in birds, in which the nerve from one optic lobe passes totally and exclusively to the eye upon the opposite side. In man, most of the fibres of the optic nerve from one side pass to the eye upon the opposite side; but a few fibres pass to the eye upon the same side, a few connect the tubercles upon the two sides, and a few connect the two eyes. It is not known whether or not, in man, the action of the tubercles in vision is exclusively crossed, as it appears to be in most of the inferior animals.

The optic lobes undoubtedly serve as the sole centres presiding over the sense of sight, and not merely as avenues of communication of this sense to the cerebral hemispheres. A positive proof of this proposition lies in the fact that the sense of sight is preserved after complete removal of the cerebrum, provided that injury of the tubercles have been carefully avoided.

We shall say nothing, in this connection, with regard to the movements of the iris, except that the reflex action by

which the size of the pupil is modified is effected through the optic lobes as nerve-centres. The mechanism of the movements of the iris and their regulation through nervous action are questions of great interest, and are somewhat complex. We have already treated of them to some extent, in connection with the physiology of the third pair of nerves, and they will be considered still more fully in the section on the special sense of sight.

Ganglion of the Tuber Annulare.

The tuber annulare, called the pons Varolii, or the mesocephalon, is situated at the base of the brain, just above the medulla oblongata. It is white externally, and contains in its interior a large admixture of gray matter. It presents both transverse and longitudinal white fibres. Its transverse fibres connect the two halves of the cerebellum. Its longitudinal fibres are connected below, with the anterior pyramidal bodies and the olivary bodies of the medulla oblongata, the lateral columns of the cord, and a certain portion of the posterior columns. Above, the fibres are connected with the crura cerebri, and pass to the brain. The superficial transverse fibres are wanting in animals in which the cerebellum has no lateral lobes.

The general properties of the tuber annulare have been demonstrated in the most satisfactory manner by Longet. In his experiments, direct excitation of the superficial transverse fibres did not produce well-marked convulsive movements, and there were no convulsions when the posterior fibres were stimulated. When galvanization was applied to the deeper anterior fibres, convulsive movements were distinct at each excitation. Stimulation of the posterior portion always produced pain. This was not constantly observed to follow irritation of the anterior portion, and, when pain occurred, it was thought to be due to irritation of the root of the fifth nerve.[1]

[1] Longet, *Traité de physiologie*, Paris, 1869, tome iii., p. 394.

The above experiments, it is true, are not as free from uncertainty as those made upon the more accessible parts of the encephalon, but, as far as they go, they tend to show that the tuber annulare is both insensible and inexcitable in its superficial anterior portion, which is composed chiefly of commissural fibres from the cerebellum; that it is excitable and probably insensible in its deeper anterior portion, which seems to be composed chiefly of descending motor conductors; and finally, that it is sensible and probably inexcitable in its posterior portion.

The tuber annulare undoubtedly acts as a conductor of sensory impressions and motor stimulus to and from the cerebrum, as we would naturally expect from the direction of its fibres, and as has been repeatedly shown by cases of disease, particularly as regards motion. In addition, however, judging from the fact that it contains numerous nodules of gray matter between fasciculi of white fibres, and that this gray matter contains cellular elements similar to those found in other nerve-centres, and from which new nerve-fibres undoubtedly originate, it would be inferred that these nodules have a distinct function, and give to the tuber annulare the properties of a nerve-centre. It will be interesting, therefore, to follow out the experiments upon this part, by which its action as a centre has been illustrated. These experiments are of two kinds: First, the removal of other encephalic ganglia, leaving only the tuber annulare, the medulla oblongata, and the cerebellum, and noting the properties or faculties retained by animals under these conditions. Experiments of this kind are tolerably definite, as we already know the general functions of most of the other encephalic ganglia. Second, to note the effects of extirpation of the tuber annulare alone.

If the cerebral hemispheres, the olfactory ganglia, the optic lobes, the corpora striata, and the optic thalami, be removed, the animal loses the special senses of smell and sight and the intellectual faculties, there is a certain amount

of enfeeblement of the muscular system, but voluntary motion and general sensibility are retained. There can be no doubt upon these points. As far as voluntary motion is concerned, an animal operated upon in this way is in nearly the same condition as one simply deprived of the cerebral hemispheres. There are no voluntary movements which show any degree of intelligence, but the animal can stand, and various consecutive movements are executed, which are entirely different from the simple reflex acts depending exclusively upon the spinal cord. The coördination of movements is perfect, unless the cerebellum be removed. As regards general sensibility, an animal deprived of all the encephalic ganglia except the tuber annulare and the medulla oblongata undoubtedly feels pain. This has been demonstrated in the most conclusive manner by Longet,[1] and has been shown even more satisfactorily by Vulpian.[2] In rabbits, rats, etc., after removal of the cerebrum, corpora striata, and optic thalami, pinching of the ear or foot is immediately followed by prolonged and plaintive cries. Both of the experimenters referred to insist upon the character of these cries as indicating the actual perception of painful impressions, and as very different from cries that are purely reflex, according to the ordinary acceptation of this term. Longet alludes to the voluntary movements and the cries observed in persons subjected to painful surgical operations, when incompletely under the influence of an anæsthetic, concerning the character of which there can be no doubt. He regards the movements as voluntary, and the cries as evidence of the acute perception of pain; but it is well known that such patients have no recollection of any painful impression, though they have apparently experienced great suffering. As far as we can judge from what we positively know of the functions of the encephalic centres, the pain under these circumstances is perceived by some nerve-centre, probably

[1] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 396.

[2] VULPIAN, *Système nerveux*, Paris, 1866, p. 542, *et seq.*

the tuber annulare, but the impression is not conveyed to the cerebrum, and is not recorded by the memory.

Taking all the experimental facts into consideration, the following seems to be the most reasonable view with regard to the function of the tuber annulare as a nerve-centre.

It is an organ capable of originating a stimulus giving rise to voluntary movements, when the cerebrum, corpora striata, and the optic thalami, have been removed, and probably regulates the automatic voluntary movements of station and progression. Many voluntary movements, the result of intellectual effort, are made in obedience to a stimulus transmitted from the cerebrum, through conducting fibres in the tuber annulare, to the motor conductors of the cord and the general motor nerves.

The tuber annulare is also capable of perceiving painful impressions, which, when all of the encephalic ganglia are preserved, are also conducted to and are perceived by the cerebrum, and are remembered; but there are distinct evidences of the perception of pain, even when the cerebrum has been removed.

Cases of disease or injury of the tuber annulare on one side in the human subject show that its action is crossed. It is a curious fact that lesions of the encephalon involving the pons may be located during life by the existence of what is known as alternate paralysis; *i. e.*, there is hemiplegia on the side opposite to the brain-lesion, attended with paralysis of the facial on the same side as the lesion, so that the facial palsy and the hemiplegia are on opposite sides of the body. We have already cited, in connection with the physiology of the facial nerve, the cases collected by Gubler, of this alternate paralysis, in illustration of the decussation of the deep fibres of origin of the facial; for when the lesion involves parts of the encephalon anterior to or above the pons, the facial paralysis is on the same side as the hemiplegia.[1] Additional cases of alternate paralysis have been

[1] See page 147.

reported by Brown-Séquard, in an elaborate memoir on the physiology and pathology of the protuberance.[1]

Medulla Oblongata.

The chief points of interest in the physiological anatomy of the medulla oblongata relate to the direction of its fibres, their connection with the gray matter embedded in its substance, and the course of the filaments of origin of certain of the cranial nerves. Concerning the deep origin of the large root of the fifth, the motor-oculi externus, facial, pneumogastric, spinal accessory, and the sublingual, we shall have nothing to say in this connection, as we have already treated of the physiological anatomy of these nerves with sufficient minuteness; and we have now to study the functions of the medulla oblongata, and particularly its action as a nerve-centre.

Physiological Anatomy of the Medulla Oblongata.—The medulla oblongata is the oblong enlargement which connects the spinal cord with the various encephalic ganglia. It is about an inch and a quarter in length, and nearly an inch broad, at its widest portion. It rests in the basilar groove of the occipital bone, extending from the atlas to the lower border of the tuber annulare, with its broad extremity above. Like the cord, it has an anterior and a posterior median fissure.

Apparently continuous with the anterior columns of the cord, are the two anterior pyramids, one on either side. Viewed superficially, the innermost fibres of these pyramids are seen to decussate in the median line; but if these fibres be traced from the cord, it is found that they come from the white substance of its lateral columns, and that none of them are derived from the anterior columns. The fibres of the external portion of the anterior pyramids come from

[1] Brown-Séquard, *Recherches sur la physiologie et la pathologie de la protubérance annulaire.—Journal de la physiologie*, Paris, 1858, tome i., p. 755, *et seq.*; and, Ibid., 1859, tome ii., p. 130, *et seq.*

the anterior columns of the cord. At the site of the decussation, the pyramids are composed entirely of white matter; but as the fibres spread out to pass to the encephalon above, they present nodules of gray matter between the fasciculi.

External to the anterior pyramids, are the corpora olivaria. These are oval, and are surrounded by a distinct groove. They are white externally, and contain a gray nucleus, called the corpus dentatum.

External to the corpora olivaria, are the restiform bodies, formed exclusively of white matter, and constituting the postero-lateral portion of the medulla. They are continuous with the posterior columns of the cord. The restiform bodies spread out as they ascend, and pass to the cerebellum, forming a great portion of the inferior peduncles.

Beneath the olivary bodies, and between the anterior pyramids and the restiform bodies, are the lateral tracts of the medulla, called by the French, the intermediary fasciculi. These are composed of an intimate mixture of white and gray matter, and have a yellowish-gray color. They receive all that portion of the antero-lateral columns of the cord which does not enter into the composition of the anterior pyramids. These are frequently considered as parts of the restiform bodies, but they are peculiarly interesting, from the fact that they contain the gray centre presiding over respiration, and for that reason we have described them as distinct fasciculi.

The posterior pyramids (fasciculi graciles) are the smallest of all. They pass upward to the cerebrum, without decussating, and are composed exclusively of white matter. As they pass upward, they diverge, leaving a space at the fourth ventricle.

The fourth ventricle is in the medulla, and is bounded above, by the valve of Vieussens and the under surface of the cerebellum. In the lower part of the floor of the fourth ventricle, are several transverse fasciculi of white matter; but the

greatest part of this portion is composed of a layer of gray substance.

The two lateral halves of the posterior portion of the medulla are connected together by fibres arising from the gray matter of the lateral tracts, or intermediary fasciculi, passing obliquely, in a curved direction from behind forward, to the raphe in the median line. There are also fibres passing from before backward, to form a posterior commissure, and fibres arising from the cells of the olivary bodies, which connect the gray substance of the lateral halves. Commissural fibres also connect the gray matter of the lateral tracts with the corpora dentata of the olivary bodies, and the olivary bodies with the cerebellum, their fibres forming part of the inferior peduncle of the cerebellum. In addition, it is probable that fibres, taking their origin from all of the gray nodules of the medulla, pass to the parts of the encephalon situated above.

As far as the fibres of origin of the nerves are concerned, it may be stated in general terms that a number of the motor roots arise from the gray matter of the floor of the fourth ventricle, the roots of the sensory nerves arising from gray matter in the posterior portions.

Aside from purely anatomical demonstrations, the connection of the anterior pyramids of the medulla with the corpora striata has been shown by pathological observations. It is well known that, when the connection between the nerve-centres and the fibres is destroyed, these fibres after a time become degenerated. In old lesions of the corpora striata, Cruveilhier, Türk, and, more lately, Vulpian, have shown that, when the white substance is injured upon one side, there follow degeneration and atrophy of the fibres of the corresponding cerebral peduncle and anterior pyramid of the medulla, and of the lateral portion of the spinal cord upon the opposite side.[1] This important fact illustrates the connection between the lateral columns of the cord and the

[1] VULPIAN, *Système nerveux*, Paris, 1866, p. 470.

anterior pyramids of the medulla oblongata, the decussation of the anterior pyramids, and the passage of fibres from the anterior pyramids to the corpora striata, in the substance of the cerebral peduncles.

Functions of the Medulla Oblongata.

It is hardly necessary to discuss the functions of the medulla oblongata as a conductor of sensory impressions and of motor stimulus to and from the brain. We know that there is conduction of this kind from the spinal cord to the ganglia of the encephalon, and this must take place through the medulla; a fact which is inevitable, from its anatomical relations, and which is demonstrated by its section in living animals. Nor is it necessary to dwell upon its general properties, in which it resembles the spinal cord, at least as far as has been demonstrated by experiments upon living animals or upon animals just killed. It is difficult to expose this part in the higher classes of animals, but the experiments of Longet[1] and of Vulpian[2] show that it is sensitive on its posterior surface and insensible in front. The difficulty of observing the phenomena which follow its irritation in living animals has rendered it impossible to determine the limits of its excitability and sensibility as exactly as has been done for the different portions of the cord.

It is also somewhat difficult to determine whether the action of the medulla itself, in its relations to motion and sensation, be crossed or direct. As regards conduction from the brain, the direction is sufficiently well shown by cases of cerebral disease, in which the paralysis, in simple lesions, is always on the opposite side of the body. Philipeaux and Vulpian have shown that, in the medulla, this crossed action is not distinct. After section of one lateral half of the medulla in dogs and Guinea-pigs, there was not complete pa-

[1] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., p. 377.

[2] VULPIAN, *Système nerveux*, Paris, 1866, p. 484.

ralysis of motion, either on one side or the other, though the animals operated upon were not able to stand.[1]

The action of the medulla as a reflex nerve-centre depends upon its gray matter. When this gray substance is destroyed, certain of the important reflex functions are instantly abolished. From its connections with various of the cranial nerves, we should expect it to play an important part in the movements of the face, in deglutition, in the action of the heart and of various glands, etc., important points which will be fully considered in their appropriate place. Its most striking function, however, is in connection with respiration.

Connection of the Medulla Oblongata with Respiration. —It did not escape the observation of Galen, that when a section was made at the summit of the spinal cord, the animal was suddenly destroyed.[2] This fact has been considered as well established, since the time of Galen, but in 1809, Legallois made a number of experiments upon rabbits, cats, etc., in which he showed that respiration depends exclusively upon the medulla oblongata and not upon the brain, and he further located the part which presides over this function at the site of origin of the pneumogastric nerves:[3] "For, if we open the cranium of a young rabbit, and extract the brain, by successive portions, from before backward, cutting it by slices, we can remove in this way all of the brain proper, and then the entire cerebellum and a part of the medulla oblongata. But it (respiration) ceases suddenly when we include in a section the origin of the eighth pair of nerves (pneumogastrics)." The experiments of Legallois were repeated and confirmed before a commission from the French Institute, composed of Von Humboldt,

[1] Vulpian, *Système nerveux*, Paris, 1866, p. 495

[2] Galenus, *De Anatomicis Administrationibus*, Liber viii., Cap. ix.—*Opera*, Lipsiæ, 1821, tomus ii., pp. 696, 697.

[3] Legallois, *Expériences sur le principe de la vie.*—*Œuvres*, Paris, 1824, tome i., p. 64. The date of these experiments is given by Legallois on page 74.

Hallé, and Percy.[1] Flourens, in his elaborate experiments upon the nerve-centres, extended the observations of Legallois, and limited the respiratory centre in the rabbit, between the upper border of the roots of the pneumogastrics and a plane situated about a quarter of an inch below the lowest point of origin of these nerves; these limits, of course, varying with the size of the animal.[2] Following these experiments, Longet has shown that the respiratory nervous centre does not occupy the whole of the medulla included between the two planes indicated by Flourens, but that it is confined to the gray matter of the lateral tracts, or the intermediary fasciculi. This was demonstrated by the fact that respiration persists in animals after division of the anterior pyramids and the restiform bodies. Subsequently, Flourens still farther restricted the limits of the respiratory centre, and fully confirmed the observations of Longet.[3]

The portion of the medulla oblongata above indicated presides over the movements of respiration, and is the true respiratory nerve-centre. Nearly all who have repeated the experiments of Flourens have found that the spinal cord may be divided below the medulla oblongata, and that all of the encephalic ganglia above may be removed, respiratory movements still persisting. It is a very common thing in vivisections to kill an animal by breaking up the medulla. In a dog, for example, we grasp the head firmly with the left hand, flex it forcibly on the neck, and penetrate with a stylet a little behind the occipital protuberance, entering between the atlas and the skull. By a rapid lateral motion of the instrument, the medulla is broken up, and the animal instantly ceases to breathe. There are no struggles, no manifestations of the distress of asphyxia; the respiratory mus-

[1] LEGALLOIS, *op. cit.*, tome i., p. 248.

[2] FLOURENS, *Système nerveux*, Paris, 1842, p. 204.

Flourens was in error when he stated (page 197) that Lorry was the first to show that animals were instantly killed by destruction of the summit of the spinal cord, for this was distinctly indicated by Galen, in the second century.

[3] LONGET, *Traité de physiologie*, Paris, 1869, tome iii., pp. 387, 388.

cles simply cease their action, and the animal loses instantly the sense of want of air. A striking contrast to this is presented when the trachea is tied or when all of the respiratory muscles are paralyzed without touching the medulla. The same phenomena follow injury to the medulla in the human subject; and in anæsthesia from the administration of chloroform, a patient will sometimes suddenly stop breathing, apparently because the medulla oblongata becomes affected.

In another volume, we have insisted upon the mechanism of the reflex phenomena of respiration. We have conclusively shown by experiments, that an impression is received by the sensory nerves of the general system, due to want of oxygen, and not to the irritation produced by carbonic acid; and that this impression is conveyed to the medulla oblongata, and gives rise to the reflex movements of respiration. If this impression be abolished, there are no respiratory movements; and if the medulla, the sole centre capable of receiving this impression and of generating the stimulus sent to the respiratory muscles, be destroyed, respiration instantly ceases, without any sensation of asphyxia.[1]

It does not seem that there can be any doubt with regard to the action of the medulla oblongata as the respiratory nervous centre; still, it has been stated by Brown-Séquard, that the commonly-accepted view is not correct; that the sudden arrest of respiratory movements following destruction of the medulla is due to irritation and not to its removal; and that, in certain cases, the movements may become reëstablished after the irritation has subsided.[2] Schiff noted, in 1852, that dogs lived for a certain time after injury of

[1] See vol. i., Respiration, p. 479, *et seq.*

Our original experiments on the respiratory sense were made in 1860–'61, and published in October, 1861. See *Experimental Researches on Points connected with the Action of the Heart and with Respiration.—American Journal of the Medical Sciences*, Philadelphia, October, 1861.

[2] Brown-Séquard, *Recherches sur les causes de mort après l'ablation de la partie de la moelle allongée qui a été nommée point vital.—Journal de la physiologie*, Paris, 1858, tome i., p. 217, *et seq.;* and, *Recherches expérimentales sur la physiologie de la moelle allongée.*—Ibid., 1860, tome iii., p. 151, *et seq.*

the so-called vital point.[1] As regards the experiments upon which the opinion of Brown-Séquard is based, we have only to say that, while a return of respiratory movements is perhaps possible in certain cold-blooded animals (which will live for weeks after extirpation of the medulla, respiring by the skin alone) the experiments on rabbits are so extraordinary, and the results obtained are so diametrically opposed to those of all other observers, that they cannot be accepted without full confirmation. As is remarked by Vulpian, if the cause of arrest of respiration in the higher animals were due, not to removal of the respiratory centre, but to simple irritation, these movements should return after the circulation had been kept up for a time by artificial respiration. This never occurs. "The possibility of reflex movements remains during all the time of pulmonary insufflation; but the respiratory movements are definitively abolished."[2] We must then adhere to the view that the medulla oblongata is the centre which presides over the respiratory movements.

To conclude our history of the influence of the medulla on respiration, we have only to refer to an interesting series of experiments recently made by Schiff, in which one lateral half of the cord just below the medulla, or the lowest part of the medulla, was divided. In these experiments, it was found that section of the lateral columns at the point of origin of the first pair of cervical nerves abolished respiratory movements upon the corresponding side of the body. In one experiment, the section was made in a dog, and all the movements, except those of respiration, remained. The abdomen was opened, and one-half of the diaphragm was seen to be entirely passive. In another experiment, exposure of the diaphragm did not affect the volume of air inspired, but after section of the lateral column on one side, the volume of air inspired was diminished by about one-third.[3]

[1] Schiff, *Lehrbuch der Physiologie*, Lahr, 1858–'59, S. 323.

[2] Vulpian, *Système nerveux*, Paris, 1866, p. 507.

[3] Schiff, *Einfluss des verlängerten Marks auf die Athmung.—Archiv für die gesammte Physiologie*, Bonn, 1870, Bd. iii., S. 624.

Vital Point.—Since it has been definitely ascertained that destruction of a restricted portion of the gray substance of the medulla produces instantaneous and permanent arrest of the respiratory movements, Flourens and others have spoken of this centre as the vital knot, the destruction of which is immediately followed by death. With our present knowledge of the properties and functions of the different tissues and organs of which the body is composed, it is almost unnecessary to present any arguments to show the unphilosophic character of such a sweeping proposition. We can hardly imagine such a thing as instantaneous death of the entire organism; still less can it be assumed that any restricted portion of the nervous system is the one essential, vital point. Probably a very powerful electric discharge passed through the entire cerebro-spinal axis produces the nearest approach to instantaneous death of any thing of which we have any knowledge; but, even here, it is by no means certain that some parts do but for a time retain their so-called vital properties. In apparent death, the nerves and the heart may be shown to retain their characteristic properties; the muscles will contract under stimulus, and will appropriate oxygen and give off carbonic acid, or respire; the glands may be made to secrete, etc.; and no one can assume that, under these conditions, the entire organism is dead. We really know of no such thing as death, except as the various tissues and organs which go to make up the entire body become so altered as to lose their physiological properties beyond the possibility of restoration; and this never occurs for all parts of the organism in an instant. A person drowned may be to all appearances dead, and would certainly die without measures for restoration; yet, in such instances, restoration may be accomplished, the period of apparent death being simply a blank, as far as the recollection of the individual is concerned. It is as utterly impossible to determine the exact instant when the vital principle, or whatever it may be called, leaves the body in death, as to indicate the time

when the organism becomes a living being. Death is nothing more than a permanent destruction of so-called vital physiological properties; and this occurs successively, and at different periods, for different tissues and organs.

When we see that frogs will live for weeks, and sometimes for months, after destruction of the medulla oblongata, and that, in mammals, by keeping up artificial respiration, we can prolong many of the most important functions, as the action of the heart, for hours after decapitation, we can understand the physiological absurdity of the proposition that there is any such thing as a vital point, in the medulla, or in any part of the nervous system.

Connection of the Medulla Oblongata with Various Reflex Acts.—There are numerous reflex phenomena that are completely under the control of the medulla oblongata as a nerve-centre. Among these are the various acts connected with respiration, as yawning, coughing, crying, sneezing, etc. It also presides over the coördination of the muscles concerned in expression, and the act of vomiting. We have seen, in treating of the pneumogastric nerves, that their galvanization arrests the action of the heart in diastole. The same result follows galvanization of the medulla at the point of origin of these nerves.[1] In another volume, we have fully discussed the influence of the medulla upon sugar formation in the liver, as illustrated by the beautiful experiments of Bernard, in which he produced diabetes in animals by irritating the floor of the fourth ventricle, and the influence of this centre upon the quantity and the composition of the urine.[2]

There is very little to be said concerning certain ganglia and other parts of the brain that we have not yet considered. The olfactory bulbs, or ganglia, preside over olfaction, and will be treated of fully in connection with the special senses.

[1] See page 225. [2] See vol. iii., Excretion, pp. 172, 323.

The pineal gland and the pituitary body, in their structure, present a certain resemblance to the ductless glands, and their anatomy has been considered in another volume.[1] Passing over the purely theoretical views of Galen, Willis, Descartes, and other of the older writers, who had very indefinite ideas of the functions of any of the encephalic ganglia, we have only to say that the uses of the pineal gland and pituitary body in the economy are entirely unknown. The same remark applies to the corpus callosum, the septum lucidum, the ventricles, hippocampi, and various other minor parts that are necessarily described in anatomical works. It is useless to discuss the early or even the recent speculations with regard to the functions of these parts, which are entirely unsupported by experimental or pathological facts, and which have not advanced our positive knowledge. Most of the parts just enumerated have no physiological history.

Rolling and Turning Movements following Injury of Certain Parts of the Encephalon.

The remarkable movements of rolling and turning, produced by section or injury of certain of the commissural fibres of the encephalon, are not very important in their bearing upon the functions of the brain, and are rather to be classed among the curiosities of experimental physiology. These movements follow unilateral lesions, and are dependent, to a certain extent, upon a consequent inequality in the power of the muscles on one side, without actual paralysis. Vulpian enumerates the following parts, injury of which, upon one side, in living animals, may determine movements of rotation:

"1. Cerebral hemispheres;
"2. Corpora striata;
"3. Optic thalami (Flourens, Longet, Schiff);
"4. Cerebral peduncles (Longet);
"5. Pons Varolii;

[1] See vol. iii., Ductless Glands, p. 364.

"6. Tubercula quadrigemina or bigemina (Flourens);

"7. Peduncles of the cerebellum, especially the middle, and the lateral portions of the cerebellum (Magendie);

"8. Olivary bodies, restiform bodies (Magendie);

"9. External part of the anterior pyramids (Magendie);

"10. Portion of the medulla from which the facial nerve arises (Brown-Séquard);

"11. Optic nerves;

"12. Semicircular canals (Flourens); auditory nerve (Brown-Séquard)."

To the parts above enumerated, Vulpian adds the upper part of the cervical portion of the spinal cord.[1]

The movements which follow unilateral injury of the parts mentioned above are of two kinds; viz., rolling of the entire body on its longitudinal axis, and turning, always in one direction, in a small circle, called by the French the movement of *manége*. They were first observed in dogs by Pourfour du Petit, who noted that animals rolled like a ball, after section of one lateral half of the cerebellum with the root of one of the peduncles;[2] but later, Magendie[3] and Flourens[4] noted the same phenomena. In 1823, a curious case of the same kind of movements in the human subject was reported by Serres.[5] It is not necessary to cite in detail the numerous experiments of this kind, made by Longet, Schiff, Brown-Séquard, Vulpian, and others, except as they have presented explanations, more or less satisfactory, of the phenomena observed.

A capital point to determine in the phenomena of rolling or turning is, whether these movements be due to paralysis

[1] Vulpian, *Système nerveux*, Paris, 1866, p. 584.

[2] Pourfour du Petit, *Nouveau système du cerveau.—Recueil d'observations d'anatomie et de chirurgie*, Paris, 1766, p. 121.

[3] Magendie, *Mémoire sur les fonctions de quelques parties du système nerveux.—Journal de physiologie*, Paris, 1824, tome iv., p. 399, *et seq.*

[4] Flourens, *Système nerveux*, Paris, 1842, p. 489.

[5] Serres, *Suite des recherches sur les maladies organiques du cervelet.—Journal de physiologie*, Paris, 1823, tome iii., p. 136.

or enfeeblement of certain muscles upon one side of the body, to a direct or reflex irritation of the parts of the nervous system involved, or to all of these causes combined. The experiments of Brown-Séquard and others conclusively show that the movements may be due to irritation alone, for they occur when parts of the encephalon and the upper portions of the cord are simply pricked, without section of fibres.[1] When there is extensive division of fibres, it is probable that the effects of the enfeeblement of certain muscles are added to the phenomena produced by simple irritation. The most satisfactory explanation of these movements is the one proposed by Brown-Séquard, who attributes them to a more or less convulsive action of muscles on one side of the body, produced by irritation of the nerve-centres. He regards the rolling as simply an exaggeration of the turning movements, and places both in the same category.[2] It is proper to state, however, that this explanation is not accepted by Longet[3] or by Vulpian,[4] both of whom have made numerous experiments with regard to the movements of rotation. In addition to the phenomena just described, Magendie has noted remarkable movements of the eyes following section of one of the peduncles of the cerebellum. "The eye of the side operated upon is directed downward and forward: that of the opposite side is fixed in a direction upward and backward, which gives to the face a curious expression."[5] Longet noted the same phenomena in dogs and rabbits after division of one of the restiform bodies.[6]

[1] Brown-Séquard, *On Turning and Rolling produced by Injuries of the Nervous System.—Experimental Researches applied to Physiology and Pathology*, New York, 1853, p. 21.

[2] Brown-Séquard, *Note sur les mouvements rotatoires.—Journal de la physiologie*, Paris, 1860, tome iii., p. 720.

[3] Longet, *Traité de physiologie*, Paris, 1869, tome iii., p. 397, *et seq.*

[4] Vulpian, *Système nerveux*, Paris, 1866, p. 594.

[5] Magendie, *Leçons sur les fonctions et les maladies du système nerveux*, Paris, 1841, tome i., p. 261.

[6] Longet, *Traité de physiologie*, Paris, 1869, tome iii., p. 392.

We do not propose to enter into an elaborate discussion of the above experiments, for the reason that they do not seem to have advanced our positive knowledge of the functions of the nerve-centres. In some of them, the movements have been observed toward the side operated upon, and in others, toward the sound side. These differences probably depend upon the fact, that in certain experiments, the fibres are involved before their decussation, and in others, after they have crossed in the median line. In some instances, the movements may be due to a reflex action, from stimulation of afferent fibres, and in others, the action of the irritation may be direct. Judging from the fact that most of the encephalic commissural fibres are apparently insensible and inexcitable under direct stimulation, it is probable that the action is generally reflex.

Though we have avoided a full discussion of the question under consideration, it is one that may be, to some, of considerable interest, from the remarkable character of the phenomena observed, and the reader is referred for further information to the elaborate chapter on this subject by Vulpian[1] and a recent article by Onimus.[2] In the latter article, there are many curious experiments upon frogs and aquatic birds.

In concluding the physiological history of the encephalon, we have only to refer to the general properties of certain of the peduncles. Longet found that direct irritation of the superior and the inferior peduncles of the cerebellum, in rabbits, produced pain, but the disturbance consequent upon exposure of the parts did not allow of any accurate observations upon the movements. He says nothing of the general properties of the middle peduncles or of the peduncles of the cerebrum.[3]

[1] Vulpian, *Système nerveux*, Paris, 1866, p. 583, *et seq.*

[2] Onimus, *Recherches expérimentales sur les phénomènes consécutifs à l'ablation du cerveau et sur les mouvements de rotation.—Journal de l'anatomie et de la physiologie*, Paris, 1870–'71, tome vii., p. 662.

[3] Longet, *Traité de physiologie*, Paris, 1869, tome iii., p. 398.

CHAPTER XV.

SYMPATHETIC NERVOUS SYSTEM.

General arrangement of the sympathetic system—Peculiarities in the intimate structure of the sympathetic ganglia and nerves—General properties of the sympathetic ganglia and nerves—Functions of the sympathetic system—Vaso-motor nerves—Reflex phenomena operating through the sympathetic system—Trophic centres and nerves, so called.

While there are certain points in the physiology of the sympathetic nervous system that are perfectly well established, it must be admitted that its functions are, in many respects, obscure, and that our positive knowledge of its general properties and its relations to the functions of nutrition, secretion, movements, etc., amounts to comparatively little. The very name, sympathetic, is some indication of our indefinite ideas with regard to its functions; but we have adopted this name, for the reason that it is the one most generally in use, though it has no very exact relation to the peculiar functions of the system. It is sometimes called the ganglionic nervous system; but this name is inappropriate, as it implies that it alone possesses ganglia. The name of the system of organic, or vegetative life is more in accordance with its general functions; but this is not so commonly used as that of sympathetic system. The older anatomists and physiologists called the great cord of this system the nervus intercostalis.

As far as we know, there is no account of the sympathetic system, even in the most recent works on physiology or in special treatises, a careful study of which does not convey

the idea that there is little else in the literature of the subject than controversial questions of priority, etc., in minor details, and a few observations, some of them quite unsatisfactory, with regard to the effects of the division or galvanization of sympathetic filaments upon the functions of circulation, secretion, and animal heat. We can hardly venture to hope that this chapter will be exceptional in this regard, unless we pass over very briefly the bibliographical discussions so elaborately presented by many authors. It is unfortunate that well-ascertained facts, which might be stated in a very few pages, should be so largely overshadowed by a mass of purely historical details of no great interest. Still, we must take the physiological data as we find them, and endeavor not to limit the knowledge to be looked for in the future, by adopting theories upon insufficient positive evidence.

There are certain important anatomico-physiological questions, more or less definitely determined, that have a direct bearing upon the functions of the sympathetic system. These are the following: Is the sympathetic anatomically and physiologically dependent upon its connections with the cerebro-spinal nerves? What are the general properties of the sympathetic nerves as regards motion and sensation? Do the sympathetic ganglia act as independent reflex nerve-centres? To what extent and in what way do the sympathetic ganglia and nerves influence the functions of the various organs and tissues to which their filaments are distributed? A solution of these questions involves a careful and critical study of the results of experiments on living animals and of pathological facts; and it is evident that very little information is to be derived from observations made anterior to the discovery of the properties and functions of the most important parts of the cerebro-spinal system. We will begin the study of these points with an account of the general arrangement and the peculiarities of structure of the sympathetic ganglia and nerves.

General Arrangement of the Sympathetic System.

Like the cerebro-spinal system, the sympathetic is composed of centres and nerves, at least as far as we can judge from its anatomy. The centres contain nerve-cells, most of which differ but little from the cells of the encephalon and spinal cord. The nerves are composed of fibres, the greater part of which are identical in structure with the ordinary motor and sensory fibres. The fibres are connected with the nerve-cells in the ganglia, and the ganglia are connected with each other by commissural fibres. These ganglia constitute a continuous double chain, on either side of the body, beginning above, by the ophthalmic ganglia, and terminating below, in the ganglion impar. It is important to note, however, that the chain of sympathetic ganglia is not independent, but that each ganglion receives motor and sensory filaments from the cerebro-spinal nerves, and that some filaments pass from the sympathetic to the cerebro-spinal centres. The general distribution of the sympathetic filaments is to mucous membranes, and possibly to integument, to non-striated muscular fibres, and particularly to the muscular coat of the arteries. As far as we have been able to learn from anatomical investigations, there are no fibres derived exclusively from the sympathetic which are distributed to striated muscles, except those which pass to the muscular tissue of the heart. Near the terminal filaments of the sympathetic, in most of the parts to which these fibres are distributed, there exist numerous ganglionic cells.

The general arrangement of the sympathetic ganglia and the distribution of the nerves may be stated, sufficiently for our purposes, very briefly; still, a knowledge of certain anatomical points is indispensable as an introduction to an intelligent study of the physiology of this system.

In the cranium, are four ganglia; the ophthalmic, the spheno-palatine, the otic, and the submaxillary. In the neck, are the three cervical ganglia; the superior, middle, and in-

ferior. In the chest, are the twelve thoracic ganglia, corresponding to the twelve ribs. The great semilunar ganglia, the largest of all, sometimes called the abdominal brain, are in the abdomen, by the side of the cœliac axis. In the lumbar region, in front of the spinal column, are the four, and sometimes five, lumbar ganglia. In front of the sacrum, are the four or five sacral, or pelvic ganglia; and in front of the coccyx, is a small, single ganglion, the last of the chain, called the ganglion impar. Thus, the sympathetic cord, as it is sometimes called, consists of from twenty-eight to thirty ganglia on either side, terminating below in a single ganglion.

Cranial Ganglia.—The ophthalmic, lenticular, or ciliary ganglion is situated deeply in the orbit, is of a reddish color, and about the size of a pin's-head. It receives a motor branch from the third pair, and sensory filaments from the nasal branch of the ophthalmic division of the fifth. It is also connected with the cavernous plexus and with Meckel's ganglion. Its so-called motor and sensory roots from the third and the fifth pair have already been described in connection with these nerves. Its filaments of distribution are the ten or twelve short ciliary nerves, which pass to the ciliary muscle and the iris. A very delicate filament from this ganglion passes to the eye with the central artery of the retina, in the canal in the centre of the optic nerve.

The functions of the ophthalmic ganglion are connected exclusively with the action of the ciliary muscle and iris; and we will here do nothing more than indicate its anatomical relations, leaving its physiology to be taken up under the head of vision.

The spheno-palatine ganglion was first described by Meckel, and is known as Meckel's ganglion.[1] This is the largest of the cranial ganglia. It is of a triangular shape,

[1] Meckel, *De Ganglio secundi Rami quinti Paris Nervorum Cerebri nuper detecto*, Herolini, 1749; in Ludwig, *Scriptores Nevrologici minores selecti*, Lipsiæ, 1795, tomus iv., p. 7.

reddish in color, and is situated in the spheno-maxillary fossa, near the spheno-palatine foramen. It receives a motor root from the facial, by the Vidian nerve. Its sensory roots are the two spheno-palatine branches from the superior maxillary division of the fifth. Its branches of distribution are quite numerous. Two or three delicate filaments enter the orbit and go to its periosteum. Its other branches, which it is unnecessary to describe fully in detail, are distributed to the gums, the membrane covering the hard palate, the soft palate, the uvula, the roof of the mouth, the tonsils, the mucous membrane of the nose, the middle auditory meatus, a portion of the pharyngeal mucous membrane, and the levator palati and azygos uvulæ muscles. It is probable that the filaments sent to these two striated muscles are derived from the facial nerve and do not properly belong to the sympathetic system.[1] They were first accurately described, with their connections, by Longet.[2] The ganglion also sends a short branch, of a reddish-gray color, to the carotid plexus.

The otic ganglion, sometimes called Arnold's ganglion, is a small, oval, reddish-gray mass, situated just below the foramen ovale. It receives a motor filament from the facial, and sensory filaments from branches of the fifth and the glosso-pharyngeal. Its filaments of distribution go to the mucous membrane of the tympanic cavity and Eustachian tube, and to the tensor tympani and tensor palati muscles. Reasoning from the general mode of distribution of the sympathetic filaments, those going to the striated muscles are derived from the facial.[3] It also sends branches to the carotid plexus.

The submaxillary ganglion was discovered by Meckel.[4]

[1] In treating of the facial (see page 161), we have shown that the movements of the levator palati and azygos uvulæ are animated by filaments derived from this nerve, which simply pass through Meckel's ganglion.

[2] Longet, *Anatomie et physiologie du système nerveux*, Paris, 1842, tome ii., p. 128.

[3] See page 154.

[4] Meckel, *De quinto Pare Nervorum Cerebri;* in Ludwig, *Scriptores Nevrologici minores selecti*, Lipsiæ, 1791, tomus i., p. 214.

It is situated on the submaxillary gland, is small, rounded, and of a reddish-gray color. It receives motor filaments from the chorda tympani, and sensory filaments from the lingual branch of the fifth. Its filaments of distribution go to Wharton's duct, to the mucous membrane of the mouth, and to the submaxillary gland.

Cervical Ganglia.—The three cervical ganglia are situated opposite the third, fifth, and the seventh cervical vertebræ respectively. The middle ganglion is sometimes wanting, and the inferior is occasionally fused with the first thoracic ganglion. These ganglia are connected together by the so-called sympathetic cord. They have numerous filaments of communication above, with the cranial and the cervical nerves of the cerebro-spinal system. Branches from the superior ganglion go to the internal carotid, to form the carotid and the cavernous plexus, following the vessels as they branch to their distribution. Branches from this ganglion pass to the cranial ganglia. There are also branches which unite with filaments from the pneumogastric and the glosso-pharyngeal to form the pharyngeal plexus, and branches which form a plexus on the external carotid, the vertebral, and the thyroid artery, following the ramifications of these vessels.

From the cervical portion of the sympathetic, the three cardiac nerves arise and pass to the heart, entering into the formation of the cardiac plexus. The superior cardiac nerve arises from the superior ganglion; the middle nerve, the largest of the three, arises from the middle ganglion, or from the sympathetic cord, when this ganglion is wanting; and the inferior nerve arises from the inferior ganglion or the first thoracic. These nerves present numerous communications with various of the adjacent cerebro-spinal nerves, penetrate the thorax, and form the deep and the superficial cardiac plexus, and the posterior and the anterior coronary plexus. In these various plexuses, are found numerous ganglioform

enlargements; and upon the surface and in the substance of the heart, are numerous collections of nerve-cells connected with the fibres, which were first accurately described and figured by Dr. Robert Lee.[1]

Thoracic Ganglia.—The thoracic ganglia are situated in the chest, under the pleura, and rest on the heads of the ribs. They are usually twelve in number, but occasionally two are fused into one. They are connected together by the sympathetic cord. They each communicate by two filaments with the cerebro-spinal nerves; one of these being white, like the spinal nerves, and probably passing to the sympathetic, and the other, of a grayish color, is thought to contain the true sympathetic filaments. From the upper six ganglia, filaments pass to the aorta and its branches. The branches which form the posterior pulmonary plexus arise from the third and fourth ganglia. The great splanchnic nerve arises mainly from the seventh, eighth, and ninth ganglia, receiving a few filaments from the upper six ganglia. This is a large, white, rounded cord, which penetrates the diaphragm and passes to the semilunar ganglion, sending a few filaments to the renal plexus and the suprarenal capsules. The lesser splanchnic nerve arises from the tenth and eleventh ganglia, passes into the abdomen, and joins the cœliac plexus. The renal splanchnic nerve arises from the last thoracic ganglion, and passes to the renal plexus. The three splanchnic nerves present numerous anastomoses with each other.

Ganglia in the Abdominal and the Pelvic Cavity.—The semilunar ganglia on the two sides send off radiating branches to form the solar plexus. They are situated by the side of the cœliac axis and near the suprarenal capsules. These are the largest of the sympathetic ganglia. From these arise numerous plexuses distributed to various

[1] LEE, *On the Ganglia and Nerves of the Heart.—Philosophical Transactions*, 1849, Part i., London, 1849.

parts in the abdomen, as follows: The phrenic plexus follows the phrenic artery and its branches, to the diaphragm. The cœliac plexus subdivides into the gastric, hepatic, and splenic plexuses, which are distributed to organs as their names indicate. From the solar plexus, different plexuses are given off, which pass to the kidneys, the suprarenal capsules, the testes, in the male, and the ovaries, in the female, the intestines, by the superior and the inferior mesenteric plexuses, the upper part of the rectum, the abdominal aorta, and the vena cava. The filaments follow the distribution of the blood-vessels in the solid viscera.

The lumbar ganglia, four in number, are situated in the lumbar region, upon the bodies of the vertebræ. They are connected with the ganglia above and below and with each other by the sympathetic cord, receiving, like the other ganglia, filaments from the spinal nerves. Their branches of distribution form the aortic lumbar plexus and the hypogastric plexus, and follow the course of the blood-vessels.

The four or five sacral ganglia and the ganglion impar are situated by the inner side of the sacral foramina and in front of the coccyx. These are connected with the ganglia above and with each other, and receive filaments from the sacral nerves, there being generally two branches of communication for each ganglion. The filaments of distribution go to all of the pelvic viscera and the blood-vessels. The inferior hypogastric, or pelvic plexus is a continuation of the hypogastric plexus above, and receives a few filaments from the sacral ganglia. The most interesting branches from this plexus are the uterine nerves, which go to the uterus and the Fallopian tubes. In the substance of the uterus, the nerves are connected with small collections of ganglionic cells, which were described in 1839, by Dr. Robert Lee.[1] The sympathetic filaments are undoubtedly prolonged into the upper and lower extremities, following the course of the blood-vessels, and are distributed to their muscular coat.

[1] LEE, *Memoir on the Ganglia and Nerves of the Uterus*, London, 1849.

According to the latest researches, the filaments of the sympathetic, at or near their termination, are connected with ganglionic cells, not only in the heart and the uterus, but in the blood-vessels, lymphatics, anal canals, the submucous and the muscular layer of the entire alimentary canal, the salivary glands, liver, pancreas, larynx, trachea, pulmonary tissue, bladder, ureters, the entire generative apparatus, suprarenal capsules, thymus, lachrymal canals, ciliary muscle, and the iris.[1] In these situations, nerve-cells have been demonstrated by various observers, and it is probable that they exist everywhere in connection with the terminal filaments of this system of nerves.

Peculiarities in the Intimate Structure of the Sympathetic Ganglia and Nerves.—The peculiarities in the structure of the cells and fibres of the sympathetic system are not numerous, nor do they possess very great physiological importance. The free communications between the sympathetic ganglia and the cerebro-spinal nerves, and the differences in the general appearance of certain of these anastomosing branches, lead to the important question of their origin. As a rule, the sympathetic nerves are softer and more grayish in color than the spinal nerves. When there are two branches of communication between a ganglion and a spinal nerve, one of them is white and the other is grayish, and we might infer from this that one, the white, is derived from the spinal system, and the other, from the sympathetic; but this is a point not yet settled by microscopical investigations. It has been conclusively shown, however, by Courvoisier, that the communicating fibres pass in both directions. Taking advantage of the degeneration of nerve-fibres after separation from their proper centres, this observer has demonstrated that, after division of the branches between the spinal nerves and the sympathetic ganglia, cer-

[1] MAYER, in STRICKER, *Handbuch der Lehre von den Geweben*, Leipzig, 1871, S. 820.

tain fibres in the end attached to the spinal nerve become degenerated, while others retain their anatomical integrity. This shows that, in all probability, the cells to which the degenerated fibres belong are in the sympathetic ganglia, and that the perfect fibres belong to the cerebro-spinal system. On the other hand, in the end attached to the sympathetic ganglia, there are degenerated fibres which belong to the spinal system, and perfect fibres attached to the sympathetic cells. According to these observations, in frogs, the fibres belonging to the spinal nerves constitute about two-thirds of the communicating branches, one-third being derived from the sympathetic system. In rabbits, the preponderance of the cerebro-spinal fibres is not so great.[1]

While the branches of the sympathetic contain a large number of the ordinary medullated fibres, such as are found in the cerebro-spinal nerves, they also present numerous fibres of Remak, and fine fibres, from $\frac{1}{10000}$ to $\frac{1}{5500}$ of an inch in diameter, which are regarded by Kölliker as true efferent fibres from the sympathetic ganglia.[2] With regard to the fibres of Remak, we have nothing to add to what we have already stated under the head of the general structure of the nervous system.[3] These points, with the fact that most of the terminal filaments of the sympathetic are connected with nerve-cells in the substance of the different tissues, constitute the most important anatomical peculiarities of the sympathetic nerve-fibres.

With regard to the cells, which constitute the characteristic anatomical element of the sympathetic ganglia, we shall have little to say, as their peculiarities at present seem to be of purely anatomical interest. They are generally rounded, ovoid, or pear-shaped, with a nucleus, generally clear, and a

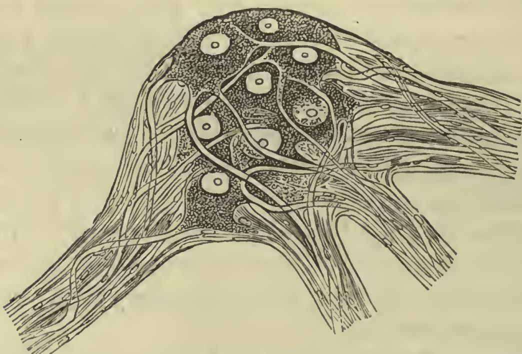
[1] COURVOISIER, *Beobachtungen über den sympathischen Gränzstrang.—Archiv für microscopische Anatomie*, Bonn, 1866, Bd. ii., S. 30, *et seq.* The method adopted in these investigations is the one already referred to, employed by Waller. (See page 80.)

[2] KÖLLIKER, *Éléments d'histologie humaine*, Paris, 1868, p. 426.

[3] See page 24.

distinct nucleolus. They present a nucleated capsule, probably composed of connective tissue, which is sometimes lined on its inner surface with a single layer of flattened, polygonal epithelium. Some of the cells are unipolar, some are bipolar, and some are multipolar. In frogs, Beale and Arnold have described a peculiar appearance in certain cells, there being a single, straight prolongation, surrounded by a fine, spiral fibre. These have not been demonstrated in the human subject, and it is not necessary to enter into a discussion of the probable origin and nature of the spiral fibre.[1] The connection between the cells and fibres of the sympathetic is probably the same as in the cerebro-spinal centres, and is represented in the accompanying diagram, taken from Leydig.

FIG. 11.



Sympathetic ganglion with multipolar cells; highly magnified. (LEYDIG, *Traité d'histologie*, Paris, 1866, p. 193.)

General Properties of the Sympathetic Ganglia and Nerves.

The older writers had no definite ideas with regard to the functions of the sympathetic system, and were divided, even, on the simple question of its sensibility, some assuming that

[1] For a full account of the spiral fibres and the peculiarities of structure of the sympathetic system, the reader is referred to the elaborate article by Mayer. (STRICKER, *Handbuch der Lehre von den Geweben*, Leipzig, 1871, S. 815.)

the ganglia were absolutely insensible, while others noted distinct evidences of pain following their irritation in living animals. Passing to the researches of the more recent observers, we find that Flourens noted evidences of pain on pinching the semilunar ganglia, in rabbits.[1] Brachet exposed the abdominal and the thoracic ganglia in calves, dogs, etc., and found them at first insensible, but pricking these parts produced pain after they had been exposed for a few minutes. The sensibility thus noted was thought by Brachet to be due to inflammation following exposure of the ganglia.[2] Müller found that mechanical or chemical irritation of the semilunar ganglia in rabbits produced pain.[3] Without discussing the observations of Bichat[4] and others, who regarded the sympathetic ganglia and nerves as entirely insensible, we will pass to the direct experiments of Longet, the results of which seem to be entirely trustworthy and satisfactory, both as regards sensibility and the property of exciting movements. In all experiments of this kind, it is of course essential to avoid direct irritation or traction of the communicating branches from the cerebro-spinal nerves. In dogs, Longet noted distinct evidences of sensibility following irritation of the semilunar ganglia, and pain after prolonged stimulation of the ganglia in the cervical and in the lumbar region, taking all precautions to avoid irritating the cerebro-spinal filaments. The sensibility of these parts, however, is dull as compared with that of the ordinary sensory nerves.[5] We have also noted a dull but well-marked sensibility of the cervical ganglia in rabbits. In view of the decided and uniform results of the most careful recent experiments on this point, there can be no doubt of the exist-

[1] Flourens, *Recherches expérimentales sur les propriétés et les fonctions du système nerveux*, Paris, 1842, p. 230.

[2] Brachet, *Recherches expérimentales sur les fonctions du système nerveux ganglionaire*, Bruxelles, 1834, p. 305, *et seq.*

[3] Müller, *Elements of Physiology*, London, 1840, vol. i., p. 712.

[4] Bichat, *Anatomie générale*, Paris, 1801, tome i., p. 227.

[5] Longet, *Traité de physiologie*, Paris, 1869, tome iii., p. 593.

ence of a certain degree of sensibility in the ganglia of the sympathetic system.

As regards excitability, recent experiments are quite satisfactory. Müller exposed the intestines and the semilunar ganglia in rabbits; and, having waited until the intestines, which generally present movements on first opening the abdomen, had ceased their contractions, the peristaltic movements "were immediately renewed with extraordinary activity" by touching the ganglia with caustic potash.[1] The experiments of Longet show that a feeble continued galvanic current applied to the great splanchnic nerves produces contractions of the muscular coat of the intestines, when they contain alimentary matters, but that no contractions occur when they are empty.[2] On the other hand, Pflüger has observed that galvanization of the splanchnic nerves produces a passive condition of the small intestine; that is, arrest of its movements without persistent contractions of its muscular coat; but these results were not confirmed in analogous experiments performed by Biffi.[3] More recently, in a series of very elaborate experiments, by Legros and Onimus, it has been shown that the induced galvanic current applied to the splanchnic nerves does not produce peristaltic movements, but that these movements are excited by the constant current.[4]

Taking into consideration the most reliable direct observations upon the sympathetic ganglia and nerves, the fact that their stimulation induces movements in the non-striated muscles to which they are distributed can hardly be doubted. This action is particularly well marked in the muscular coat of the blood-vessels; but here, the function of the nerves is so important, that it merits special consideration, and will

[1] MÜLLER, *Elements of Physiology*, London, 1840, vol. i., p. 713.

[2] LONGET, *Traité de phyisologie*, Paris, 1869, tome iii., p. 595; and, *Anatomie et physiologie du système nerveux*, Paris, 1842, tome ii., p. 568.

[3] PFLÜGER ET BIFFI, *Sur une système qui suspend les mouvements de l'intestin grêle.—Journal de la physiologie*, Paris, 1858, tome i., p. 421.

[4] LEGROS ET ONIMUS, *Recherches expérimentales sur les mouvements de l'intestin.—Journal de l'anatomie*, Paris, 1869, tome vi., p. 196.

be treated of fully under the head of the vaso-motor nerves. The mechanism of these movements, however, is peculiar. The action does not immediately follow the stimulation, as it does in the case of the cerebro-spinal nerves and the striated muscles, but is induced gradually, beginning a few seconds after the irritation, endures for a time, and is more or less tetanic.[1] This mode of action is peculiar to the sympathetic nerves and the non-striated muscular fibres.

When we remember the invariable connection of the sympathetic ganglia with the cerebro-spinal nerves, we see at once the importance of the question of the derivation of the motor and sensory properties of the ganglionic system. Are the sympathetic ganglia independent nerve-centres, or do they derive their properties from the cerebro-spinal system? This question may be satisfactorily answered by two kinds of experimental facts: In the first place, section or irritation of the spinal cord and certain of the encephalic centres is capable of influencing the vaso-motor system, a fact which will be dwelt upon more fully in another connection. In the second place, the experiments of Bernard upon the submaxillary ganglion and its influence on the secretion of the submaxillary gland have demonstrated, in the most conclusive manner, that this ganglion is the centre presiding immediately over the reflex phenomena of secretion by the gland; but it has also been shown that, when all of the connections of the submaxillary ganglion with the cerebro-spinal system are divided, after a few days, this ganglion loses its power as a reflex nervous centre.[2] In the volume on secretion, we have given numerous examples of reflex action through the sympathetic system.[3] The experiments just cited from Bernard show that individual ganglia belonging to this system may act independently for a time; but that this action can-

[1] LEGROS ET ONIMUS, *De la contraction des muscles de la vie végétative.—Journal de l'anatomie*, Paris, 1869, tome vi., p. 433.

[2] BERNARD, *Recherches expérimentales sur les nerfs vasculaires et calorifiques.—Journal de la physiologie*, Paris, 1862, tome v., pp. 407, 410.

[3] See vol. iii., Secretion, p. 28, *et seq.*

not remain indefinitely, after the cerebro-spinal branches have been divided. It remains, however, to apply these experiments to other sympathetic ganglia; but, in the case of the submaxillary, they are very satisfactory, from the facility with which the parts may be operated upon, and the certainty with which the ganglion may be separated from its connections with the cerebro-spinal system. As regards the explanation of the final loss of power over the functions of the submaxillary gland, the experiments of Waller seem to have escaped the attention of the eminent physiologist whom we have quoted. There is no experimental fact more conclusively demonstrated than that of the anatomical degeneration and consequent loss of physiological function of nerve-fibres in a few days after they have been separated from their centres of origin. After division of a cerebro-spinal nerve-trunk, the tubes soon lose their anatomical characters, and will no longer respond to a galvanic stimulus. In the case of the fibres operating upon the submaxillary gland, the question of their degeneration after division of the cerebro-spinal roots was not submitted to microscopical investigation. If these fibres had undergone the degeneration which has so frequently been observed in experiments upon other nerves, their galvanization would not have produced any effect; which was precisely the result obtained by Bernard. In the absence of direct observations upon this point, it is the most reasonable view to adopt, that the fibres from the cerebro-spinal nerves had lost their function, as a natural consequence of separation from their centres, and that this was the cause of the absence of effect upon the gland following their galvanization. The observation of Bernard shows, however, that filaments may pass to special organs from the cerebro-spinal centres through the sympathetic ganglia.

Functions of the Sympathetic System.

In the early part of the last century (1712 and 1725), Pourfour du Petit demonstrated that the influence of the

sympathetic nerve in the neck (the great sympathetic was frequently called the nervus intercostalis) was propagated from below upward toward the head, and not from the brain downward. This may be taken as the starting-point of our definite knowledge of the functions of the sympathetic system, though the experiments of Petit only showed the influence of the cervical portion upon the eye.[1] In 1816, Dupuy removed the superior cervical ganglia in horses, with the effect of producing injection of the conjunctiva, increase of temperature in the ear, and an abundant secretion of sweat upon one side of the head and neck.[2] These experiments showed that the sympathetic has an important influence on nutrition, calorification, and secretion. In 1851, Bernard repeated the experiments of Pourfour du Petit, dividing the sympathetic in the neck on one side in rabbits, and noted, on the corresponding side of the head and the ear, increased vascularity, and an elevation in temperature, amounting to from 7° to 11° Fahr. This condition of increased heat and vascularity continues for several months after division of the nerve.[3] In 1852, Brown-Séquard repeated these experiments,

[1] PETIT, *Mémoire dans lequel il est démontré que les nerfs intercostaux fournissent des rameaux qui portent des esprits dans les yeux.—Mémoires de l'académie royale des sciences*, Année 1727, Paris, 1729, p. 5, *et seq.*

[2] DUPUY, *Versuche über die Wegnahme des ersten Halsknotens des Ganglionnerven bei Pferden* (*Aus Leroux's Journ. de Médec.*, t. xxxvii., 1816, pp 340–350).—*Deutsches Archiv für die Physiologie*, Halle und Berlin, 1818, Bd. iv., S. 105, *et seq.*

We have been unable to consult the article by Dupuy in the original, but the reference in Meckel's *Archiv* gives a full account of the experiments and conclusions. In one experiment, it is stated that, after removal of the ganglia on both sides, in a horse, already feeble and emaciated, the face and ears became hot and moist. Dupuy does not seem to have attached much importance to the elevation in temperature. In his conclusions, he states that "the consequences of destruction of the ganglia are, constriction of the pupils, redness of the conjunctiva, general emaciation, as well as œdema of the extremities and a general cutaneous eruption. The ganglionic nerve appears to have a great influence upon nutrition."

[3] BERNARD, *Influence du grand sympathique sur la sensibilité et sur la calorification.—Comptes rendus de la société de biologie*, Paris, 1851, tome iii., p. 163.

and attributed the elevation of temperature directly to an increase in the supply of blood to the parts affected. He made a most important advance in the history of the sympathetic, by demonstrating that its section paralyzed the muscular walls of the arteries, and, farther, that galvanization of the nerve in the neck caused the vessels to contract. This was the discovery of the vaso-motor nerves, concerning which so much has been written within the past few years, and it belongs without question to Brown-Séquard, who published his observations in August, 1852.[1] A few months later, in the same year, Bernard made analogous experiments, and presented the same explanation of the phenomena observed.[2]

The above embraces all that is important with regard to the history of experimental observations upon the sympathetic. It is evident that we could know nothing of the functions of this system before the time of Pourfour du Petit, when the prevailing opinion was that the nerve originated from the encephalon, and that its influence was propagated downward; and the writings of Bichat, Brachet, Tiedemann, and others, published anterior to the experiments of Bernard and of Brown-Séquard, present interesting suggestions and theories, but contain little that bears upon our positive knowledge.

The important points developed by the first experiments of Bernard and of Brown-Séquard were, that the sympathetic influences the general process of nutrition, and that many of its filaments are distributed to the muscular coat of the blood-vessels. Before these experiments, it had been shown that filaments from this system influenced the contractions

[1] BROWN-SÉQUARD, *Experimental Researches applied to Physiology and Pathology.—The Medical Examiner*, Philadelphia, August, 1852, New Series, vol. viii., p. 489. In 1839, Valentin referred to filaments of the sympathetic distributed to the blood-vessels and influencing their calibre (VALENTIN, *De Functionibus Nervorum Cerebralium et Nervi Sympathetici*, Bernæ, 1839, p. 153, *et seq.*).

[2] BERNARD, *Sur les effets de la section de la portion céphalique du grand sympathique.—Compte rendu des séances de la société de biologie pendant le mois de novembre*, Paris, 1852, tome iv., p. 169.

of the muscular coats of the alimentary canal. Leaving, for the present, the action of the vaso-motor nerves, we will briefly recapitulate some of the facts with regard to the influence of the sympathetic upon animal heat and secretion.

When the sympathetic is divided in the neck, the local increase in temperature is always attended with a very great increase in the supply of blood to the side of the head corresponding to the section. The increased temperature is due to a local exaggeration of the nutritive processes, apparently dependent directly upon the hyperæmia; and it is not probable that there are any nerves to which the name of calorific, as distinguished from vaso-motor, can justly be applied. There are numerous instances in pathology of local increase in temperature attending increased supply of blood to restricted parts.

The experiment of dividing the sympathetic in the neck, especially in rabbits, is so easily performed, that the phenomena observed by Bernard and Brown-Séquard have been repeatedly verified. We have often done this in class-demonstrations. A very striking experiment is the following, suggested by Bernard:[1] After dividing the sympathetic and exhibiting the increase in the temperature and the vascularity of the ear on one side in the rabbit, if both ears be cut off just above the head with a sharp knife, the artery on the side on which the sympathetic has been divided will frequently send up a jet of blood to the height of several feet, while, on the sound side, the jet is always much less forcible, and may not be observed at all. This experiment succeeds best in large rabbits.

It is very easy to observe the effects of dividing the sympathetic in the neck, but analogous phenomena have been noted in other parts. Among the most striking of these experiments are those reported by Samuel, who noted an intense hyperæmia of the mucous membrane of the stomach

[1] BERNARD, *Recherches expérimentales sur les nerfs vasculaires et calorifiques du grand sympathique.—Journal de la physiologie*, Paris, 1862, tome v., p. 397.

and intestines following extirpation of the cœliac plexus. By comparative experiments, it was shown that this did not result from the peritonitis produced by the operation.[1]

As regards secretion, the influence of the sympathetic is very marked. When the sympathetic filaments distributed to a gland are divided, the supply of blood is very much increased, and an abundant flow of the secretion follows. This point we have already discussed in another volume, and have referred particularly to the experiments of Bernard upon the salivary glands.[2] In some recent experiments by Peyrani, it has been shown that the sympathetic has a remarkable influence over the secretion of urine. When the nerves are galvanized in the neck, the amount of urine and urea is increased, and this increase is greater with the induced than with the constant current. When the sympathetic is divided, the quantity of urine and urea sinks to the minimum.[3]

Since the publication of our volume on secretion, Dr. Moreau has published a series of observations on the influence of the sympathetic nerves upon the secretion of liquid by the intestinal canal, which are peculiarly interesting in their bearing upon the sudden occurrence of watery diarrhœa. In these experiments, the abdomen was opened in a fasting animal, and three loops of intestine, each from four to eight inches long, were isolated by two ligatures. All of the nerves passing to the middle loop were divided, taking care to avoid the blood-vessels. The intestine was then replaced, and the wound in the abdomen was closed with sutures. The next day the animal was killed. The two loops with the nerves intact were found empty, as is normal in fasting animals, and the mucous membrane was dry; but the loop with the nerves divided was found filled with a

[1] SAMUEL, *Principes fondamentaux de l'histoire du système nerveux nutritif.—Journal de la physiologie*, Paris, 1860, tome iii., p. 580.

[2] See vol. iii., Secretion, p. 28, *et seq.*

[3] PEYRANI, *Le sympathique par rapport à la sécrétion des urines.—Comptes rendus*, Paris, 1870, tome lxx., p. 1300.

clear, alkaline liquid, colorless or slightly opaline, which precipitated a few flocculi of organic matter on boiling.[1]

Vaso-Motor Nerves.

The experiments which we have already cited demonstrate beyond a doubt the existence of nerves distributed to the muscular coats of the blood-vessels, and capable of regulating their calibre and the quantity of blood sent to different parts. These are the vaso-motor nerves, discovered by Brown-Séquard, in 1852.[2] The importance of nerves capable of regulating what we may call the local circulations is sufficiently apparent. The glands, for example, require at certain times an immense increase in their supply of blood, and the same is probably true of the muscles, brain, and other parts. It has been shown, by direct experiments upon living animals, that local variations in the circulation, independent of the action of the heart, actually take place, and that they are of great importance in special functions; and there are numerous instances of such action, which can only take place through the nervous system. The phenomena of blushing and pallor, from mental emotions, are familiar examples.

There can be no doubt of the fact that the sympathetic branches contain filaments capable of modifying the calibre of the blood-vessels, and that the cerebro-spinal nerves also contain elements possessing analogous properties; but when we reflect upon the extensive anastomoses, in both directions, between the sympathetic and the ordinary motor and sensory nerves, we can appreciate the importance of determining the exact origin and course of these vaso-motor fibres. The first important question is, whether the vaso-motor filaments be derived from the sympathetic ganglia or from the cerebro-spinal centres.

All experiments upon the question just proposed tend to

[1] MOREAU, *Expériences physiologiques sur l'intestin.—Bulletin de l'académie impériale de médecine*, Paris, 1860, tome xxxv., p. 388.

[2] See page 432.

show that the vaso-motor nerves are derived exclusively from the cerebro-spinal system, and do not originate in the sympathetic ganglia. Without citing the numerous confirmatory observations of different physiologists, it is sufficient to state that Schiff has experimentally demonstrated, in the most conclusive manner, that the vaso-motor nerves are derived from the cerebro-spinal centres and not from the sympathetic ganglia.[1] There is now no difference of opinion among physiologists upon this point, the only question being the exact location of the vaso-motor centres. Ludwig and Thiry found that section of the cord in the upper cervical region produced dilatation of most of the blood-vessels of the organism, but notably of the mesenteric vessels, and that galvanization of the cord at its lower cut extremity caused the vessels to contract.[2] These observations have been repeatedly confirmed.

As a summary of our present knowledge of the origin of the vaso-motor nerves in the cerebro-spinal axis, we may cite the following remarks, from a review of the experiments of Schiff, by Brown-Séquard: "1. That if there are vaso-motor elements which decussate in the spinal cord, their number is excessively small. 2. That the facts observed by M. Schiff, on this subject, admit of a more simple explanation. 3. That a number of the vaso-motor elements stop in the spinal cord. 4. That a tolerably large number of vaso-motor elements, coming from different points in the body, ascend as far as the tuber annulare, and some as far as the cerebellum and to other parts of the encephalon. 5. That consequently, the medulla oblongata is not the sole source of the vaso-motor elements."[3] These statements express pretty much all that we know of the origin of the vaso-motor elements and their decussation, as far as their

[1] SCHIFF, *Untersuchungen zur Physiologie des Nervensystems*, Frankfurt am Main, 1855, S. 167, *et seq.*

[2] LUDWIG UND THIRY, *Über den Einfluss des Halsmarkes auf den Blutstrom.—Sitzungs-berichte der mathematischnaturwissenschaftlichen Classe der kaiserlichen Akademie der Wissenschaften*, Wien, Bd. xlix., ii Abtheilung, S. 421, *et seq.*

[3] *Journal de la physiologie*, Paris, 1858, tome i., p. 214.

direct action is concerned; but some important points have been developed by observations on reflex vaso-motor phenomena, involving a transmission of impressions to the centres through the nerves of general sensibility.

Reflex Phenomena operating through the Sympathetic System.—We shall not discuss, in this connection, the reflex phenomena of secretion, as these have already been considered with sufficient minuteness in another volume,[1] nor again treat of reflex action, through the sympathetic, upon the general circulatory system, which has been taken up fully under the head of the depressor-nerve of the circulation, described by the brothers Cyon,[2] but shall here describe certain reflex acts, involving vaso-motor phenomena, which we thus far have touched upon very briefly.

In treating of animal heat, the phenomena of which are intimately connected with the supply of blood to the parts, we have mentioned the observations of Brown-Séquard and Lombard, who found that pinching of the skin on one side was attended with a diminution in the temperature in the corresponding member of the opposite side, and that sometimes, when the irritation was applied to the upper extremities, changes were produced in the temperature of the lower limbs. Tholozan and Brown-Séquard found, also, that lowering the temperature of one hand produced a considerable depression in the heat of the other hand, without any notable diminution in the general heat of the body. Brown-Séquard showed that by immersing one foot in water at 41° Fahr., the temperature of the other foot was diminished about 7° Fahr. in the course of eight minutes.[3] These facts show that certain impressions made upon the sensory nerves affect the animal heat by reflex action. As section of the sympathetic filaments increases the heat in particular parts, with an increase in the supply of blood, and their galvaniza-

[1] See vol. iii., Secretion, p. 32.

[2] See page 229.

[3] See vol. iii., Nutrition, p. 416.

tion reduces the quantity of blood and diminishes the temperature, it is reasonable to infer that the reflex action takes place through the vaso-motor nerves. If we assume that the impression is conveyed to the centres by the nerves of general sensibility, and that the vessels are modified in their calibre and the heat is affected through the sympathetic fibres, we have only to determine the situation of the centres which receive the impression and generate the stimulus. These centres, as we have already seen, are not located in the sympathetic ganglia, but in the cerebro-spinal axis.

In this connection, we may quote a curious observation by Schiff, which he brings forward to illustrate the influence of the brain in certain acts, probably operating through the sympathetic system: "It is undisputed that psychical acts are determined by the brain. If we bring a dog and a cat together, their psychical irritation is manifested more especially therein that the hair of the dog on his back, of the cat on her tail, stands up. Now, if we destroy, in the cat, the lumbar portion of the spinal cord, and bring her together with a strange dog, the hair of the tail will still rise. If we leave the spinal nerves intact, the hair of the cat's tail will remain smooth, even though she be attacked by a dog."[1]

From all of these observations, and others of the same kind which we have not thought it necessary to quote, the existence of vaso-motor nerves and their connection with centres in the cerebro-spinal axis are sufficiently well established. It is certain, also, that centres presiding over particular functions may be located, as the genito-spinal centre, in the spinal cord opposite the fourth lumbar vertebra, and the cilio-spinal centre, in the cervical region of the cord, both described by Budge.[2] A stimulus generated in these

[1] SCHIFF, *The Independence of the Sympathetic.—Journal of Psychological Medicine*, New York, 1871, vol. v., p. 587.

[2] BUDGE, *Lehrbuch der speciellen Physiologie des Menschen*, Leipzig, 1862, S. 510, 767.

In a recent review of the theory proposed by Cyon; viz., that the true vaso-motor centres are located in the encephalon, above the medulla oblongata and

centres, sometimes as the result of impressions received through the nerves of general sensibility, produces contraction of the non-striated muscular fibres of the iris,[1] vasa deferentia, etc., including the muscular walls of the blood-vessels. The contraction of the muscular walls of the vessels is tonic; and when their nerves are divided, relaxation takes place, and the vessels are dilated by the pressure of blood. By this action, the local circulations are regulated in accordance with impressions made on sensory nerves, the physiological requirements of certain parts, mental emotions, etc. Secretion, the peristaltic movements of the alimentary canal, the movements of the iris, etc., are influenced in this way. This action is also illustrated in cases of reflex paralysis, in inflammations as the result of "taking cold," and in many pathological conditions, of which it is not our province to treat. The facts already noted with regard to the excito-motor action of the spinal cord in the functions of animal life have their analogy in the vaso-motor reflex system. When the centres are destroyed, when the sensory nerves are paralyzed by anæsthetics, or when the true vaso-motor nerves are divided, reflex vaso-motor action is abolished.

The vaso-motor filaments are not confined to the branches of the sympathetic, but they exist as well in the ordinary cerebro-spinal nerves. Bernard has demonstrated this fact in the most conclusive manner. He divided the fourth, fifth, sixth, seventh, and eighth pairs of lumbar nerves on one side in a dog, at the spinal column, and paralyzed mo-

the cerebellum, and that no effects upon the blood-vessels following irritation of the sensory nerves are observed when the encephalon is extirpated, leaving the medulla and cerebellum, or when the sensory nerves are paralyzed by anæsthetics, Heidenhain presents positive results in opposition to the negative observations of Cyon, at least as far as the experiments after removal of the superior parts of the encephalon are concerned. (HEIDENHAIN, *Ueber Cyon's neue Theorie der centralen Innervation der Gefässnerven.—Archiv für die gesammte Physiologie*, Bonn, 1871, Bd. iv., S. 551, *et seq.*)

[1] We assume that dilatation of the iris is produced by the contraction of radiating fibres. Their existence, however, is denied by some anatomists. We will discuss this question fully under the head of vision.

tion and sensation in the leg of that side, but the temperature of the two sides remained the same. He afterward exposed and divided the sciatic nerve on that side, and then noted a decided increase of temperature.[1] This experiment, which is only one of a large number, shows conclusively that the ordinary mixed nerves contain vaso-motor fibres, which are entirely independent of the nerves of motion and sensation, a fact which is admitted by all physiologists, and has frequently been illustrated in cases of disease in the human subject.

It only remains to show that the phenomena following section of the sympathetic in animals are illustrated in certain cases of disease or injury in the human subject. It is excessively rare to observe traumatic injury confined to the sympathetic in the neck. A single case, however, apparently of this kind, has lately been reported by Mitchell. A man received a gunshot-wound in the neck. Among the phenomena observed a few weeks after, were, contraction of the pupil on the side of the injury, and, after exercise, flushing of the face upon that side. There was no difference in the temperature upon the two sides, during repose, but no thermometric observations were made when half of the face was flushed by exercise.[2] Dr. Bartholow has reported several cases of unilateral sweating of the head, two observed by himself, in several of which there was probably compression of the sympathetic from aneurism. In those cases in which the condition of the eye was observed, the pupil was found contracted in some and dilated in others. In none of these cases, were there any accurate thermometric observations.[3] In a series of observations by Wagner, upon the head of a woman, eighteen minutes after decapitation, pow-

[1] BERNARD, *Recherches expérimentales sur les nerfs vasculaires et calorifiques du grand sympathique.—Journal de la physiologie*, Paris, 1862, tome v., p. 389.

[2] MITCHELL, *Injuries of Nerves*, Philadelphia, 1872, p. 318.

[3] BARTHOLOW, *Unilateral Sweating of the Head.—Quarterly Journal of Psychological Medicine*, New York, 1869, vol. iii., p. 134, *et seq.*

erful galvanization of the sympathetic produced great enlargement of the pupil.[1] In such a case as this, it would not be possible to make any observations on the influence of the sympathetic upon the temperature.

Trophic Centres and Nerves, so called.

We have deferred the consideration of the so-called trophic nerves until we had treated of the functions of the sympathetic system, because the vaso-motor nerves, by their influence upon the circulation, are evidently connected with the phenomena of nutrition. It is not necessary to dwell very minutely upon this point; but cases of disease, as well as experiments upon the inferior animals, show that when a muscle is paralyzed, as a result of the abolition of nervous influence and consequent disease, it becomes atrophied, its fibres lose their characteristic structure, and finally become incapable of contracting under any stimulus. As we have seen that the cerebro-spinal nerves, in addition to their motor and sensory fibres, contain vaso-motor elements, it becomes a question whether the muscles be supplied with special nerves, aside from those of motion and sensation and the vaso-motor nerves, which preside over their nutrition. Such could properly be called trophic nerves. Many pathologists, relying upon the presence of certain lesions of cells in the cord, in connection with cases of progressive muscular atrophy, admit the existence of trophic cells and nerves. It must be admitted, however, that these views rest upon pathological facts alone, and have not been demonstrated by physiological experiments or observations.

After what we have said, it is evident that proper nutrition of the muscular system depends upon its exercise and the integrity of its motor nerves. In the second place, the history of monsters shows that the muscular system may be

[1] WAGNER, *Note sur quelques expériences sur la partie cervicale du nerf sympathique chez une femme décapitée.—Journal de la physiologie*, Paris, 1860, tome iii., p. 175.

developed independently of the cerebro-spinal centres. In the admirable work of Brachet, on the ganglionic system, numerous cases of anencephalic[1] monsters are detailed, taken from Morgagni, Wepfer, Ruisch, Littré, Lallemand, Roux, Fauvel, Méry, Saviard, Rouhaud, Schellhase, Heyshan, Bayle, Lordat, Saint-Hilaire, and others, in which the muscular system was found more or less perfectly developed. In some of these, the fœtus was delivered at term and lived for several hours. In the case reported by Bayle, the child was born with two teeth and lived for seven days. Heyshan reported a case that lived for six days. When we consider the great number of cases of this kind on record, a few of which only are cited by Brachet, it is evident that the cerebro-spinal centres are not absolutely necessary to development *in utero*. Some of the cases reported presented spasmodic movements of certain muscles.[2]

While it is certain that a fœtus may become developed *in utero*, when there is reason to suppose that the cerebro-spinal influence is wanting and the chief nervous operations are effected through the ganglionic system, direct experiments upon the sympathetic in animals do not positively show any influence upon nutrition, except as this system of nerves affects the supply of blood to the parts. When we divide a sympathetic nerve, there is an apparent exaggeration of the nutritive processes in particular parts, and there may be inflammatory phenomena, but atrophy of muscles is not observed. Indeed, we only have atrophy of muscles following division of cerebro-spinal nerves, or, as recently-

[1] The term anencephalic is here used in the sense in which it was employed by Saint-Hilaire, as signifying absence of the encephalon and spinal cord, or the entire cerebro-spinal axis. It is sometimes applied to cases of absence of the encephalon, which are more commonly called acephalous.

[2] BRACHET, *Recherches expérimentales sur les fonctions du système nerveux ganglionaire*, Bruxelles, 1834, p. 103, *et seq.*

At the time the work of Brachet was written, it presented an admirable account of the physiology of the sympathetic system; but it antedates the positive facts ascertained by Bernard, Brown-Séquard, and other writers, to whom we have made frequent reference.

observed cases of disease have shown, after disorganization of cells belonging to what we recognize as motor centres. As regards the latter condition, there can be no doubt of the fact that progressive muscular atrophy is attended with disorganization of certain of the motor cells of the spinal cord.

Without fully discussing this subject, which belongs to pathology, the facts may be briefly stated as follows: We may have progressive atrophy of certain muscles, which may be uncomplicated with paralysis, except in so far as there is weakness of these muscles, due to partial and progressive destruction of their contractile elements. The only pathological condition in these cases, aside from the changes in the muscular tissue, is destruction of certain cells in the antero-lateral portions of the cord, with more or less atrophy of the corresponding anterior roots. No one has pretended to have demonstrated cells in the cord, presenting anatomical peculiarities by which they may be distinguished from the ordinary motor or sensory elements, but the fact of the degeneration of certain cells, others remaining normal, and this fact alone, has led to the distinction, by certain writers, of trophic cells; and, of course, these must be connected with the muscles by trophic nerves.[1]

We shall now study the phenomena of progressive muscular atrophy from a physiological point of view, and see if they afford any positive evidence of the existence of special

[1] Cases of progressive muscular atrophy have recently been studied with great minuteness, and connected with lesions of certain cells in the cord, by various authors; among whom may be mentioned, Hayem (*Note sur un cas d'atrophie musculaire progressive avec lésions de la moelle.—Archives de physiologie*, Paris, 1869, tome ii., pp. 263, 391); Charcot and Joffroy (*Deux cas d'atrophie musculaire progressive avec lésions de la substance grise et des faisceaux antéro-lateral de la moelle épinère.*—Ibid., pp. 354, 629, 744); and Duchenne and Joffroy (*De l'atrophie aiguë et chronique des cellules nerveuses de la moelle et du bulbe rachidien.*—Ibid., 1870, tome iii., p. 499).

For a full account of the disease in question, with its relations to the degeneration of nerve-cells, the reader is referred to HAMMOND, *Diseases of the Nervous System*, New York, 1871 p. 663, *et seq.*

cells and nerves presiding over the nutrition of the muscular system, or whether the phenomena observed cannot be explained by the partial degeneration of the ordinary motor cells and nerves.

There can be no doubt of the fact that the cells of the antero-lateral columns of the spinal cord preside over motion, and that the stimulus generated in these cells is conveyed to the muscles by the anterior roots of the spinal nerves. It is a fact, no less definite, that when a muscle or a part of a muscle is deprived of the motor stimulus by which it is brought into action, its fibres atrophy, become altered in structure, and lose their contractility. Starting with these two well-defined physiological propositions, and assuming that a few of the ordinary motor cells of the cord are destroyed—we will not call them trophic cells—what are the phenomena to be expected as a consequence of such a lesion? Reasoning from what we know of the physiology of the nervous system, we should expect to find the following conditions:

The destruction of certain motor nerve-cells would certainly produce degeneration of the fibres to which they give origin. This has been observed; for, in this condition, the anterior roots arising from the diseased portions of the cord are atrophied. This occurs when any motor nerves are separated from their cells of origin, and there is no necessity of assuming the existence of special trophic cells or nerves.

If a few of the motor cells be affected with disease, and the degeneration be gradual and progressive, we should expect progressive and partial paralysis of the muscles to which their nerves are distributed. This paralysis, confined to a limited number of fibres of particular muscles or sets of muscles, would give the idea of progressive weakening of the muscles, and the phenomena would not be those observed in complete paralysis, produced by section of the motor nerves. These are precisely the phenomena observed in progressive muscular atrophy, preceding the paralysis,

which is the final result of the disease, and these do not involve the action of any special centres or nerves.

As regards the muscular atrophy itself, if the nervous stimulus be progressively destroyed, the muscular tissue will necessarily undergo degeneration and atrophy.

With the above considerations, we leave the trophic cells and nerves to the pathologist, and can only admit the existence of centres and nerves specially and directly influencing the nutrition of the muscular system, when it has been demonstrated that there are lesions of particular structures in the nervous system, which produce phenomena that cannot be explained by our knowledge of the action of ordinary motor and sensory nerves and of the vaso-motor system.[1]

We have thus endeavored to represent what is actually known concerning the sympathetic system, but it is evident that we have much to learn with regard to its physiology. The great sympathetic ganglia may have functions of which we have no definite idea; and we are better prepared to advance our knowledge in this direction, by admitting our ignorance, than by attempting to supply the deficiencies in our positive information by theories unsupported by facts.

[1] We have discussed the question of the existence of trophic nerves from a physiological point of view only. In a late review of the subject, by Dr. Handfield Jones, the same opinion is expressed, based upon pathological arguments, as will be seen by the following quotation:

"In conclusion, I may state that my review of the subject leads me to discredit very much the doctrine that there exists a special class of trophic nerves; inasmuch as all the phenomena, to explain which their existence might be invoked, seem to be fairly explicable by alterations in the condition of those which have been long familiar to us." (HANDFIELD JONES, *Are there Special Trophic Nerves?—St. George's Hospital Reports*, London, 1868, vol. iii., p. 109.)

CHAPTER XVI.

SLEEP.

General considerations—Condition of the organism during sleep—Dreams—Reflex mental phenomena during sleep—Condition of the brain and nervous system during sleep—Theories of sleep—Anæsthesia and sleep produced by pressure upon the carotid arteries—Differences between natural sleep, and stupor and coma—Regeneration of the brain-substance during sleep—Theory that sleep is due to a want of oxygen—Condition of the various functions of the organism during sleep.

WHEN we remember that about one-third of our existence is passed in sleep, and that, at this time, voluntary motion, sensation, the special senses, and various of the functions of the organism, are greatly modified, the importance of a physiological study of this condition is sufficiently apparent. The subject of sleep is most appropriately considered in connection with the nervous system, for the reason that the most important modifications in function are observed in the cerebro-spinal axis and nerves. Repose is as necessary to the nutrition of the muscular system as proper exercise; but repose of the muscles relieves the fatigue due to exercise, without sleep. It is true that after violent and prolonged exertion, there is frequently a desire for sleep, but simple repose will often restore the muscular power. After the most violent effort, a renewal of muscular vigor is most easily and completely effected by rest without sleep, a fact familiar to all who are accustomed to athletic exercises. The glands engaged in the production of the true secretions need certain intervals of repose; but this does not necessarily involve

sleep. After prolonged and severe mental exertion, however, or after long-continued muscular effort which involves an excessive expenditure of the so-called nerve-force, sleep becomes an imperative necessity. If the nervous system be not abnormally excited by effort, sleep follows moderate exertion as a natural consequence, and is the only physiological means of complete restoration; but the two most important muscular acts; viz., those concerned in circulation and respiration, are never completely arrested, sleeping or waking, though they undergo certain modifications.

In infancy and youth, when the organism is in process of development, sleep is more necessary than in adult life or old age. The infant does little but sleep, eat, and digest. In adult life, under perfectly physiological conditions, we require about eight hours of sleep; some persons need less, but very few require more. In old age, unless after extraordinary exertion, less sleep is required than in adult life. Each individual learns by experience how much sleep is necessary for perfect health, and there is nothing which more completely incapacitates one for mental or muscular effort, especially the former, than loss of rest.

Sleeplessness is one of the most important of the predisposing causes of certain forms of brain-disease, a fact which is well recognized by practical physicians. One of the most refined and exquisite methods of torture is long-continued deprivation of sleep; and persons have been known to sleep when subjected to acutely painful impressions. Severe muscular effort, even, may be continued during sleep. In forced marches, regiments have been known to sleep while walking; men have slept soundly in the saddle; persons will sometimes sleep during the din of battle; and other instances illustrating the imperative demand for sleep after prolonged vigilance might be cited.[1] It is remarkable, also, how noises

[1] For a number of curious and interesting examples of sleep under the most unfavorable circumstances, the reader is referred to the admirable work of Dr Hammond (*Sleep and its Derangements*, Philadelphia, 1869, p. 14, *et seq.*).

to which we have become accustomed will fail to disturb our natural rest. Those who have been long habituated to the endless noise of a crowded city frequently find difficulty in sleeping in the oppressive stillness of the country. We must have sleep; and this demand is so imperious, that we soon accommodate ourselves to the most unfavorable surrounding conditions. It is remarkable, also, that prolonged exposure to intense cold induces excessive somnolence, and if this be not resisted, the sleep passes into stupor, the power of resistance to cold becomes rapidly diminished, and death is the inevitable result. Intense heat often produces drowsiness, but, as is well known, is not favorable to natural sleep. We generally sleep less in summer than in winter, though in summer, perhaps, we are less capable of protracted mental and physical exertion.

Sleep is preceded by an indescribable feeling of drowsiness, an indisposition to mental or physical exertion, and a general relaxation of the muscular system. It then requires a decided effort to keep awake; and if we yield to the soporific tendency, the voluntary muscles cease to act, the lids are closed, we cease to appreciate the ordinary impressions of sound, and we sometimes pass into a dreamless condition, in which we lose all knowledge of existence. We say sometimes, because the mind is not generally inactive during what we may regard as normal sleep. We may have dreams which are not due, as far as can be ascertained, to impressions from the external world received during sleep. Ideas in the form of dreams may be generated in the brain from impressions previously received while awake, or trains of thought may be gradually extended from the moments immediately preceding sleep into the insensible condition. During the nine years that we have been almost unremittingly engaged in the preparation of this work, we have frequently labored during sleep for an entire night—to no purpose, it is true—upon difficult questions to which we had devoted a great deal of thought.

There may be, during sleep, mental operations of which we have no consciousness or recollection, unconscious cerebration, as it is called by Carpenter.[1] It is well known that we vividly remember dreams immediately on awakening, but that the recollection of them rapidly fades away, unless they be brought to mind by an effort to remember and relate them. Whatever be the condition of the mind in sleep, if the sleep be normal, there is a condition of repose of the cerebro-spinal system and an absence of voluntary effort, which restore the capacity for mental and physical exertion.

The impressionability and the activity of the human mind are so great, most of the animal functions are so subordinate to its influence, and we are so subject to unusual mental conditions, that it is difficult to determine with exactness the phenomena of sleep that are absolutely physiological, and to separate those that are slightly abnormal. We cannot assert, for example, that a dreamless sleep, in which our existence is, as it were, a blank, is the only normal condition of repose of the system; nor can we determine what dreams are due to previous trains of thought, to impressions from the external world received during sleep, and are purely physiological, and what are due to abnormal nervous influence, disordered digestion, etc. We may assume that an entirely refreshing sleep is normal, and that is all.

That reflex ideas originate during sleep, as the result of external impressions, there can be no doubt; and we have already alluded to this point under the head of reflex action.[2] The most remarkable experiments upon the production of dreams of a definite character, by subjecting a person during sleep to peculiar influences, are those of Maury. The hallucinations produced in this way are called hypnagogic,[3] and

[1] CARPENTER, *Principles of Human Physiology*, Philadelphia, 1853, p. 784.

[2] See page 300

[3] From its derivation, this term is properly applied only to phenomena observed at the instant when we fall asleep, or when we are imperfectly awakened, and not to the period of most perfect repose.

they occur when the subject is not in a condition favorable to sound sleep. The experiments made by Maury upon himself are so curious and interesting, that we quote the most striking of them in full:[1]

FIRST OBSERVATION.—"I was tickled with a feather successively on the lips and inside of the nostrils. I dreamed that I was subjected to a horrible punishment, that a mask of pitch was applied to my face, and then roughly torn off, tearing the skin of the lips, the nose, and the face.

SECOND OBSERVATION.—"A pair of pincers is held at a little distance from my ear, and rubbed with a steel scissors. I dreamed that I heard the ringing of bells; this soon became the tocsin, and I imagined myself in the days of June, 1848.

THIRD OBSERVATION.—"I was caused to inhale Cologne-water. I dream that I am in a perfumer's shop, and the idea of perfumes doubtless awakens the idea of the East: I am in Cairo, in the shop of Jean Marie Farina. Many extravagant adventures follow, the connection of which escapes me.

FOURTH OBSERVATION.—"I am caused to smell a burning match. I dream that I am at sea (remark that the wind was then blowing in through the windows), and that the Saint-Barbe blew up.

FIFTH OBSERVATION.—"I am slightly pinched on the nape of the neck. I dream that a blister is applied, which recalls the recollection of a physician who had treated me in my infancy.

SIXTH OBSERVATION.—"A piece of hot iron is held to my face, keeping it far enough removed, so that the sensation of heat should be slight. I dream of *chauffeurs*, who enter houses and force the inmates, by putting their feet to the fire, to reveal where their money was. The idea of the *chauffeurs* immediately suggests that of the Duchess d'Abrantès, who, I suppose in my dream, has taken me as

[1] MAURY, *Le sommeil et les rêves*, Paris, 1865, p. 132, *et seq.*

secretary. I had, indeed, long ago read in the memoirs of this intelligent woman certain details concerning the *chauffeurs.*

Seventh Observation.—"The word *parafagaramus* is pronounced in my ear. I hear nothing, and awake, having had rather a vague dream. The experiment is repeated when I am asleep in my bed, and the word *maman* is pronounced many times in succession. I dream of different things, but in this dream I heard the humming of bees. The same experiment, repeated several days after, when I was scarcely asleep, was more conclusive. The words *Azor*, *Castor*, *Léonore*, were pronounced in my ear; on awaking, I recollected that I had heard the last two words, which I attributed to one of the persons who had conversed with me in my dream.

"Another experiment of the same kind likewise showed that the sound of the word, and not the idea attached to it, had been perceived. The words *chandelle*, *haridelle*, were pronounced in my ear many times in succession. I awoke suddenly of my own accord, saying, *c'est elle.* It was impossible for me to recall what idea I attached to this answer.

Eighth Observation.—"A drop of water is allowed to fall on my forehead. I dream that I am in Italy, that I am very warm, and that I am drinking the wine of Orviette.

Ninth Observation.—"A light, surrounded with a red paper, is many times in succession passed before my eyes. I dream of a tempest of lightning, and all the remembrance of a violent storm which I had encountered in the English Channel, in going from Morlaix to Havre, is present in my mind."

As regards dreams due to external impressions, it is a curious fact, which has been noted by many observers, and one which accords with the personal experience of all who have reflected upon the subject, that trains of thought and imaginary events, which seem to pass over a long period of time in our dreams, actually occur in the brain within a

few seconds. A person is awakened by a certain impression, which undoubtedly gives rise to a dream that seems to occupy hours or days, and yet the period of time between the impression and the awakening is hardly more than a few seconds; and persons will drop asleep for a very few minutes, and yet have dreams, with the most elaborate details, and apparently of great length. It is unnecessary to cite the numerous accounts of literary compositions of merit, the working out of difficult mathematical problems in dreams, etc., some of which are undoubtedly accurate. If it be true, that the mind is capable of forming consecutive ideas during sleep, which can hardly be doubted, there is no good reason why these phenomena should not occur, and the thoughts should not be remembered and noted, immediately on awakening. In most dreams, however, the mind is hardly in a normal condition, and the brain generally loses the power of concentration and of accurate reasoning. We sometimes commit atrocious crimes in our dreams, without appreciating their enormity, and are often placed in the most absurd and impossible conditions, without any idea, at the time, of their extraordinary and unnatural character. This is a fact sufficiently familiar to every one, and is one which does not admit of satisfactory explanation.

We have made no attempt to offer an explanation of the curious psychological phenomena presented during sleep, and, indeed, we know little enough of the action of the mind at any time; but we have merely given the above as examples of what we may call reflex mental phenomena. Somnambulism, general anæsthesia, sleep from hypnotics, the so-called magnetic sleep, ecstasy, catalepsy, trance, etc., are abnormal conditions, which we will only consider in so far as they resemble natural sleep.

Condition of the Brain and Nervous System during Sleep.

As we have already seen, during sleep, the brain may be in a condition of absolute repose, at least, as far as we have

any subjective knowledge of mental operations, or we may have more or less connected trains of thought. There is, also, as a rule, absence of voluntary effort, though movements may be made, to relieve discomfort from position or external irritation, without awakening. The sensory nerves retain their properties, though the general sensibility is somewhat blunted; and the same may be said of the special senses of hearing, smell, and probably of taste. The peculiar dreams, induced in the case of Maury by red lights, show that the sense of sight is not entirely lost. There is every reason to believe, however, that the functions of the sympathetic system are not disturbed or affected by sleep, if we except the action of the vaso-motor nerves upon the circulation in the brain.

Two opposite theories have long been in vogue with regard to the immediate cause of sleep. In one, this condition is attributed to venous congestion and increased pressure of blood in the brain, and this view probably had its origin in the fact that cerebral congestion induces stupor or coma. Stupor and coma, however, are entirely distinct from natural sleep; for here, the functions of the brain are suspended, there is no consciousness, no dreaming, and the condition is manifestly abnormal. In animals rendered comatose by opium, the brain may be exposed and is found deeply congested with venous blood. The same condition often obtains in profound anæsthesia from chloroform, but a state of the brain very nearly resembling normal sleep is observed in anæsthesia from ether. These facts have been positively demonstrated by experiments upon living animals, and have been observed in the human subject, in cases of injury of the head. When opium is administered in large doses, the brain is congested during the condition of stupor or coma, but this congestion is relieved when the animal passes, as sometimes happens, from the effects of the agent into a natural sleep.[1] In view of these facts, and others which will be stated hereafter, it is unnecessary to

[1] HAMMOND, *Sleep and its Derangements*, Philadelphia, 1869, pp. 26, 32.

discuss the theory that sleep is attended with, or is produced by, congestion of the cerebral vessels.

The idea that the circulation in the brain is diminished during sleep has long been entertained by certain physiologists; but until within a few years, it has rested chiefly upon theoretical considerations. We find this view enunciated by Blumenbach, in the following words: "These remote causes may induce the *proximate* cause, which, upon mature consideration, I think probably consists in a diminished or impeded flow of oxygenated (arterial) blood to the brain, for that fluid is of the highest importance, during the waking state, to the reaction of the sensorium upon the senses and voluntary motions." This opinion was not entirely theoretical, as is seen by the following statement: "Besides other phenomena which accord with this explanation, one is very remarkable which I witnessed in a living person, and has been already noticed—that of the brain sinking whenever he was asleep, and swelling again with blood the moment he awoke."[1]

Passing over arguments by the older writers, for and against this theory of sleep, we come to the researches of Durham, in 1860, in which it was clearly demonstrated that the supply of blood to the brain is always greatly diminished during sleep. These experiments were made upon dogs. A piece of the skull, about the size of a shilling, was removed with a trephine, and a watch-glass was accurately fitted to the opening and cemented at the edges with Canada balsam. When the animals operated upon in this way were awake, the vessels of the pia mater were seen moderately distended, and the circulation was active; but during perfectly natural sleep, the brain retracted and became pale. "The contrast between the appearances of the brain during its period of functional activity, and during its state of repose or sleep was most remarkable."[2] These observations were confirmed in

[1] Blumenbach, *The Institutions of Physiology*, Philadelphia, 1817, pp. 178, 179.

[2] Durham, *The Physiology of Sleep.—Guy's Hospital Reports*, Third Series, London, 1860, vol. vi., p. 153, *et seq.*

the most satisfactory manner by Prof. Hammond, who, in 1854, noted the changes in the circulation during sleep in a man who had a large opening in the skull from a railroad-accident. These observations were made independently of those of Durham, but were not published until some time after.[1] Prof. Hammond cites numerous observations illustrating the diminished circulation in the brain during sleep, in the human subject, which it is unnecessary to refer to in detail, and this fact may now be considered as definitively settled.[2] He also devised an instrument for measuring the extent of the cerebral pressure. This instrument consists of a brass tube, which is screwed into an opening made in the skull, and is connected with a small glass tube filled with colored water. The lower end of the brass tube is covered with a thin sheet of rubber, which rests on the brain, the cerebral pressure being marked by the height of the liquid in the glass tube. In experiments made with this apparatus, Prof. Hammond fully confirmed the results of his previous observations.[3]

The influence of diminished supply of blood to the brain has been illustrated by compression of both carotid arteries. In an experiment performed on his own person, Dr. Fleming produced immediate and profound sleep in this way, and this result invariably followed in subsequent trials upon himself and others.[4] We have already alluded to the observations of Waller, who produced anæsthesia in patients by pressure upon both pneumogastric nerves; but, as we then remarked, the nerves are so near the carotid arteries that they could hardly be compressed, in the human subject,

[1] HAMMOND, *Sleep and its Derangements*, Philadelphia, 1869, p. 37, *et seq.*

[2] An interesting case of exposure of the brain in the human subject is reported by Dr. Brown (*American Journal of the Medical Sciences*, New Series, Philadelphia, 1860, vol. xl., p. 400).

[3] HAMMOND, *op. cit.*, Appendix.

[4] FLEMING, *Note on the Induction of Sleep and Anæsthesia by Compression of the Carotids.—British and Foreign Medico-Chirurgical Review*, London, 1855, vol. xv., p. 529.

without interfering with the current of blood, and such experiments do not positively show whether the loss of sensibility be due to pressure upon the nerves or upon the vessels.[1] An important observation bearing upon this point is the following, cited by Prof. Hammond: In a lady affected with cirsoid aneurism of the scalp, both carotids were tied at different times, one by the late Dr. J. Kearney Rogers, and the other by Prof. W. H. Van Buren. "No peculiar symptoms were observed in consequence of these operations, except the supervention of persistent drowsiness, which was especially well marked after the last operation, and which, even now, is at times quite troublesome." The last operation was performed seven years ago.[2] The bearing of these facts is sufficiently evident. They all go to show that the supply of blood to the brain is very much diminished during natural sleep, and that sleep may be induced by retarding the cerebral circulation by compressing the vessels of supply. When the circulation is interfered with by compressing the veins, congestion is the result, and we have stupor or coma.

If diminished flow of blood through the cerebral vessels be the cause of natural sleep, it becomes important to inquire how this condition of physiological anæmia is brought about. It must be, that when the system requires sleep, the vessels of the brain contract in obedience to a stimulus received through the sympathetic system of nerves, diminishing the

[1] See page 256.

[2] Hammond, *op. cit.*, p. 42.

Ligation of both carotids, when the patient recovers from the operation, does not always induce drowsiness, which is probably due to free collateral circulation, by which, in some cases, the full supply of blood to the brain is maintained. In a remarkable case published by Mussey, both carotids were tied for aneurism, one being operated upon about six weeks after the other. In this case, it is remarked that "at no period subsequently to the operation of tying the second carotid, with the exception of the faintness and debility which occurred from the actual loss of blood on the removal of the tumor, has there been a single symptom of deficiency of blood in the brain." (Mussey, *Case of Aneurism by Anastomosis, in which both the Primitive Carotid Arteries were tied.—American Journal of the Medical Sciences*, Philadelphia, 1829, vol. v., p. 316.)

supply of blood, here, as in other parts, under varied physiological conditions. The vessels of the brain are provided with vaso-motor nerves, and it is sufficient to have noted that the arteries are contracted during sleep, the mechanism of this action being well established by observations upon other parts of the circulatory system. Contraction of the vessels of the pia mater has been observed by Nothnagel and others, though there is some discussion with regard to its exciting cause.[1]

It must be acknowledged that we know but little of the intimate nature of the processes of nutrition of the brain during its functional activity and in repose; but there can be no doubt of the fact that there is more or less cerebral action at all times when we are awake. Though the mental processes are much less active during sleep, even at this time, the operations of the brain are not always suspended. It is equally well established, that exercise of the brain is attended with physiological waste of nervous substance, and, like other parts of the organism, its tissue requires periodic repose to allow of the regeneration of the substance consumed. Analogies to this are to be found in parts that are more easily subjected to direct observation. The muscles require repose after exertion, and the glands, when not actively engaged in discharging their secretions, present intervals of rest.[2] As regards the glands, during the intervals of repose, the supply of blood to their tissue is very much diminished. It is probable, also, that the muscles in action receive more blood than during rest; but it is mainly when these parts are not active, and when the supply of blood is smallest, that the processes of regeneration of tissue seem to be most efficient. As a rule, the functional activity of parts, while it is attended

[1] A reference to these experiments is to be found in the *Journal of Anatomy and Physiology*, Cambridge and London, 1871, vol. v., p. 401.

[2] Luys has compared the condition of repose of the brain, with its diminished supply of blood, to the period of inactivity of the glands (*Recherches sur le système nerveux*, Paris, 1865, p. 450).

with an increased supply of blood, is a condition more or less opposed to the process of repair, the hyperæmia being, apparently, a necessity for the marked and powerful manifestations of their peculiar functions. When the parts are in active function, the blood seems to be required to keep at the proper standard the so-called irritability of the tissues, and to increase their power of action under proper stimulus. Exercise increases the power of regeneration and favors full development, in the repose which follows; but during rest, the tissues have time to appropriate new matter, and this does not seem to involve a large supply of blood. A muscle is exhausted by prolonged exertion; and the large quantity of blood passing through it carries away carbonic acid, urea, and other products of disassimilation, which are all increased in amount, until it gradually uses up its capacity for work. Then follows repose; the supply of blood is reduced, but, under normal conditions, the tissue repairs the waste which has been excited by action; the blood furnishing nutritive matter and carrying away a comparatively small amount of effete products.

We may safely assume that processes analogous to those just described take place in the brain. By absence of voluntary effort, we allow the muscles time for rest and for the repair of physiological waste, and their active function is for the time suspended. As the activity of the brain involves consciousness, volition, the generation of thought, and, in short, the mental condition observed while awake, complete repose of the brain is characterized by the opposite conditions. It is true that we rest the brain without sleep, by abstaining from mental effort, by the gratification of certain of the senses, and by mental distraction of various kinds, and that the mind may work to some degree during sleep; but during the period of complete repose, that condition which is so necessary to perfect health and full mental vigor, we lose consciousness, volition, there is no thought, and the brain, which does not receive blood enough to stimulate it

to action, is simply occupied in the insensible repair of its substance and is preparing itself for future work. The exhaustion of the muscles produces a sense of fatigue of the muscular system, indisposition to muscular exertion, and a desire for rest, not necessarily involving drowsiness; fatigue of the brain is manifested by indisposition to mental exertion, dulness of the special senses, and a desire for sleep. Simple repose will relieve physiological fatigue of muscles; and, when a particular set of muscles has been used, the fatigue disappears when these muscles alone are at rest, though others be brought into action. Sleep, and sleep alone, relieves fatigue of the brain. When the sleep has continued long enough for the rest of the brain and the repair of its tissue, we awake, prepared for new effort.

We have now only to refer to a new theory of sleep, proposed by Sommer. Taking as a basis the researches of Pettenkofer and Voit on respiration, Sommer advances the idea that, when the brain is active, or while we are awake, the system appropriates but a small quantity of oxygen in respiration, and eliminates a relatively large proportion of carbonic acid; after a time, the oxygen thus appropriated is consumed, and the system demands a new supply; during sleep, the organism appropriates oxygen largely, and eliminates a relatively small amount of carbonic acid. When the elimination of carbonic acid at the expense of the oxygen stored up reaches a certain point, the necessity for a farther supply of oxygen induces sleep; and when, during sleep, oxygen has been appropriated in sufficient quantity, the system awakes, prepared for a new period of activity of the animal functions.[1]

By reference to the researches of Pettenkofer and Voit, we find that these observers, in experiments on a man confined in a chamber in which the interchanges of gases in respiration could be estimated, noted, in twenty-four hours,

[1] SOMMER, *Neue Theorie des Schlafes.—Zeitschrift für rationelle Medicin*, Dritte Reihe, Leipzig und Heidelberg, 1868, Bd. xxxiii., S. 214, *et seq.*

that the subject of the observation, awake, but in a condition of complete repose, appropriated sixty-seven per cent. of the entire amount of oxygen of the twenty-four hours during the night, and thirty-three per cent. during the day, while he eliminated fifty-eight per cent. of the entire amount of carbonic acid excreted, during the day, and forty-two per cent. during the night. When the subject of the experiment worked during the day, by turning a heavy wheel, the appropriation of oxygen was thirty-one per cent. for the day, and sixty-nine per cent. for the night; the elimination of carbonic acid was sixty-nine per cent. for the day, and thirty-one per cent. for the night. According to these observations, the system stores up oxygen at night for use during the day, at this time eliminating a relatively small quantity of carbonic acid; and, during the day, excretes more carbonic acid than during sleep, appropriating then a relatively small amount of oxygen.[1]

This theory of sleep seems to rest upon observations too restricted to be adopted without reserve. It is stated, indeed, that the first experiments of Pettenkofer and Voit were not confirmed in other observations made upon the same person.[2] It is hardly possible, with our present infor-

[1] PETTENKOFER UND VOIT, *Ueber Kohlensäureausscheidung und Sauerstoffaufnahme während des Wachens und Schlafens beim Menschen.—Annalen der Chemie und Pharmacie*, Leipzig und Heidelberg, 1867, Bd. cxli., S. 300, 303.

[2] *Journal of Anatomy and Physiology*, Cambridge and London, 1868, vol. ii., p. 181.

The statement alluded to above is to be found in the report on physiology, by Drs. Rutherford, Gamgee, and Frazer (*loc. cit.*), but there is no indication where the new observations of Pettenkofer and Voit were published. We find no allusion to any experiments later than those published in 1867 in the *Annalen der Chemie und Pharmacie*, in *Schmidt's Jahrbücher*, from that date to the present time. In an article by these authors on the excretions, etc., observed in a patient affected with leucocythemia, it appears that the smallest difference in the appropriation of oxygen during the day and at night, in a healthy person, was fifty-one per cent. for the day, and forty-nine per cent. at night, which is so slight a variation, that it may practically be disregarded. (PETTENKOFER UND VOIT, *Ueber den Stoffverbrauch bei einem leukämischen Manne.—Zeitschrift für Biologie*, München, 1869, Bd. v., S. 327.)

mation, to assume that sleep is due simply to want of oxygen, and it is more in accordance with well-established physiological facts to attribute it to a necessity for the general regeneration of the nervous tissue, though into this, the necessity for oxygen may enter as one element in the physiological repair.

During sleep, nearly all of the functions, except those directly under the control of the sympathetic nervous system, are diminished in activity. The circulation is slower, and the pulsations of the heart are less frequent, as well as the respiratory movements. These points have already been considered under the heads of circulation and respiration. We have but little positive information with regard to the relative activity of the processes of digestion, absorption, and secretion, during sleep. The drowsiness which many persons experience after a full meal is probably due to a determination of blood to the alimentary canal, and a consequent diminution in the supply to the brain.

INDEX.

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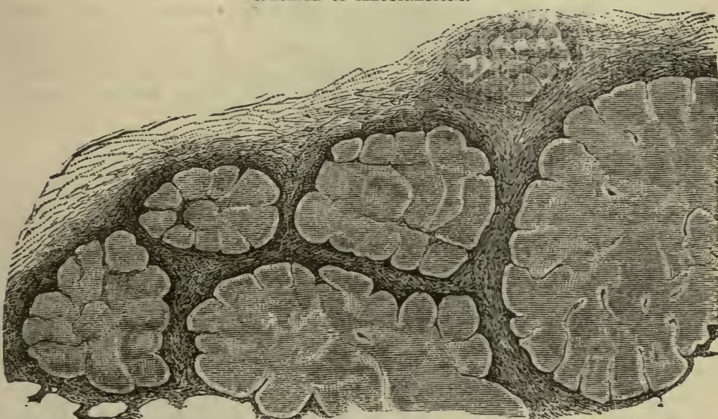

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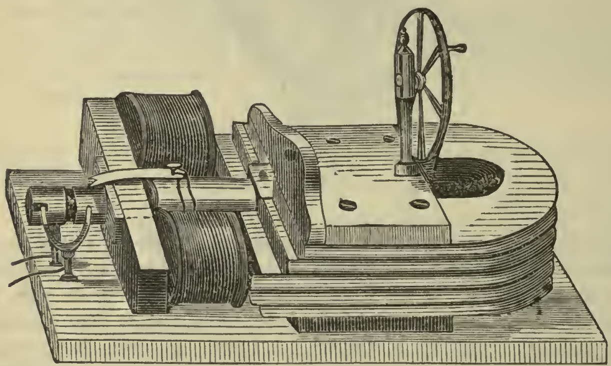

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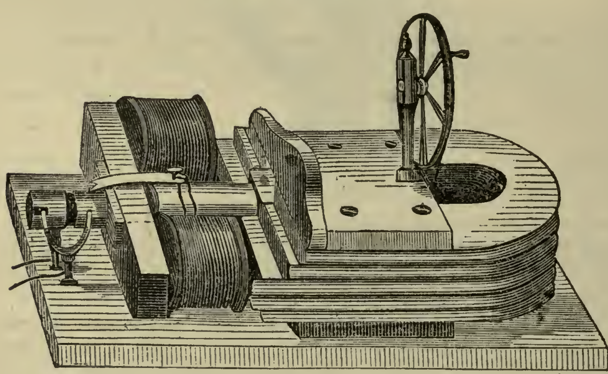

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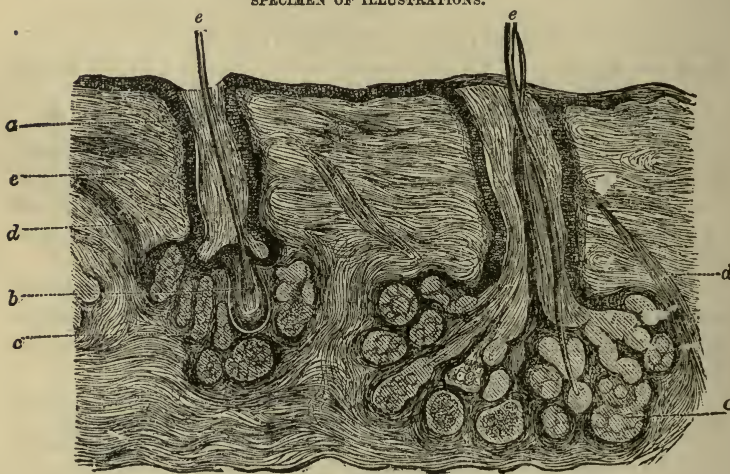

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